Charles Schwab

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THE HUMAN BODY

ITS STRUCTURE AND ACTIVITIES AND THE CONDITIONS OF ITS HEALTHY WORKING

BY

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ELEVENTH EDITION, THOROUGHLY REVISED

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PREFACE TO THE ELEVENTH EDITION

THE last few years have seen much progress in Physiology. Many new facts have been discovered and many obscure points made clearer. The reviser has made an earnest effort to incorporate in the new edition all important discoveries; he has also recast the accounts of the various bodily processes to bring them into line with present-day interpretations. This has involved rewriting large sections of the physiological part of the book. The general plan of presentation has not been changed, however, the arrangement adopted at the first revision of the present series (9th Edition) having proved reasonably satisfactory. Several new figures have been introduced; a few are original, the others used by permission of various authors and publishers. Individual acknowledgments are printed with the figures themselves. I wish to record here my appreciation of the courtesies thus extended.

E. G. M.

STANFORD UNIVERSITY,
July, 1926.

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PREFACE TO THE FIRST EDITION

In the following pages I have endeavored to give an account of the structure and activities of the Human Body, which, while intelligible to the general reader, shall be accurate, and sufficiently minute in details to meet the requirements of students who are not making Human Anatomy and Physiology subjects of special advanced study. Wherever it seemed to me really profitable, hygienic topics have also been discussed, though at first glance they may seem less fully treated of than in many School or College Text-books of Physiology. Whoever will take the trouble, however, to examine critically what passes for Hygiene in the majority of such cases will, I think, find that, when correct, much of it is platitude or truism: since there is so much that is of importance and interest to be said it seems hardly worth while to occupy space with insisting on the commonplace or obvious.

It is hard to write a book, not designed for specialists, without running the risk of being accused of dogmatism, and some readers will, no doubt, be inclined to think that, in several instances, I have treated as established facts matters which are still open to discussion. General readers and students are, however, only bewildered by the production of an array of observations and arguments on each side of every question, and, in the majority of cases, the chief responsibility under which the author of a text-book lies is to select what seem to him the best supported views, and then to state them simply and concisely: how wise the choice of a side has been in each case can only be determined by the discoveries of the future.

Others will, I am inclined to think, raise the contrary objection that too many disputed matters have been discussed: this was deliberately done as the result of an experience in teaching Physiology which now extends over more than ten years. It would have been comparatively easy to slip over things still uncertain and subjects as yet uninvestigated, and to represent our knowledge of the workings of the animal body as neatly rounded off at all its contours and complete in all its details—*totus, teres, et rotundus.* But by so doing no adequate idea of the present state of physi-

ological science would have been conveyed; in many directions it is much farther traveled and more completely known than in others; and, as ever, exactly the most interesting points are those which lie on the boundary between what we know and what we hope to know. In Gross Anatomy there are now but few points calling for a suspension of judgment; with respect to Microscopic Anatomy there are more; but a treatise on Physiology which would pass by, unmentioned, all things not known but sought, would convey an utterly unfaithful and untrue idea. Physiology has not finished its course. It is not cut and dried, and ready to be laid aside for reference like a specimen in an Herbarium, but is comparable rather to a living, growing plant, with some stout and useful branches well raised into the light, others but part grown, and many still represented by unfolded buds. To the teacher, moreover, no pupil is more discouraging than the one who thinks there is nothing to learn; and the boy who has "finished" Latin and "done" Geometry finds sometimes his counterpart in the lad who has "gone through" Physiology. For this unfortunate state of mind many Text-books are, I believe, much to blame: difficulties are too often ignored, or opening vistas of knowledge resolutely kept out of view: the forbidden religions may be, it is true, too rough for the young student to be guided through, or as yet pathless for the pioneers of thought; but the opportunity to arouse the receptive mental attitude apt to be produced by the recognition of the fact that much more still remains to be learned—to excite the exercise of the reasoning faculties upon disputed matters—and, in some of the better minds, to arouse the longing to assist in adding to knowledge, is an inestimable advantage, not to be lightly thrown aside through the desire to make an elegantly symmetrical book. While I trust, therefore, that this volume contains all the more important facts at present known about the working of our Bodies, I as earnestly hope that it makes plain that very much is yet to be discovered.

A work of the scope of the present volume is, of course, not the proper medium for the publication of novel facts; but, while the "Human Body," accordingly, professes to be merely a compilation, the introduction of constant references to authorities would have been out of place. I trust, however, that it will be found throughout imbued with the influence of my beloved master, Michael

Foster; and on various hygienic topics I have to acknowledge a special indebtedness to the excellent series entitled *Health Primers.*

The majority of the anatomical illustrations are from Henle's *Anatomie des Menschen,* and a few from Arendt's *Schulatlas,* the publishers of each furnishing electrotypes. A considerable number, mainly histological, are from *Quain's Anatomy,* and a few figures are after Bernstein, Carpenter, Frey, Haeckel, Helmholtz, Huxley, McKendrick, and Wundt. About thirty, chiefly diagrammatic, were drawn specially for the work.

Quantities are throughout expressed first on the metric system, their approximate equivalents in American weights and measures being added in brackets.

H. N. M.

Baltimore, October, 1880.

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THE HUMAN BODY

THE HUMAN BODY

CHAPTER I

THE GENERAL STRUCTURE AND COMPOSITION OF THE HUMAN BODY

Definitions. The living Human Body may be considered from either of two aspects. Its structure may be especially examined, and the forms, connections and mode of growth of its parts be studied, as also the resemblances or differences in such respects which appear when it is compared with other animal bodies. Or the living Body may be more especially studied as an organism presenting definite properties and performing certain actions; and then its parts will be investigated with a view to discovering what duty, if any, each fulfills. The former group of studies constitutes the science of Anatomy, and in so far as it deals with the Human Body alone, of *Human Anatomy;* while the latter, the science concerned with the uses—or in technical language the *functions*—of each part is known as *Physiology*. Closely connected with physiology is the science of *Hygiene,* which is concerned with the conditions which are favorable to the healthy action of the various parts of the Body; while the activities and structure of the diseased Body form the subject matter of the science of *Pathology*.

Tissues and Organs. Histology. Examined merely from the outside our Bodies present a considerable complexity of structure. We easily recognize distinct parts as head, neck, trunk and limbs; and in these again smaller constituent parts, as eyes, nose, ears, mouth; arm, forearm, hand; thigh, leg and foot. We can, with such an external examination, go even further and recognize different materials as entering into the formation of the larger parts. Skin, hair, nails and teeth are obviously different substances; simple examination by pressure proves that internally there are harder and softer solid parts; while the blood that flows from a cut finger shows that liquid constituents also exist in the Body. The conception of complexity which may be thus arrived at from external observation of the living, is greatly extended by dissection

of the dead Body, which makes manifest that it consists of a great number of diverse parts or *organs*, which in turn are built up of a limited number of materials; the same material often entering into the composition of many different organs. These primary building materials are known as the *tissues*, and that branch of anatomy which deals with the characters of the tissues and their arrangement in various organs is known as *Histology;* or, since it is mainly carried on with the aid of the microscope, as *Microscopic Anatomy*. If, with the poet, we compare the Body to a house, we may go on to liken the tissues to the bricks, stone, mortar, wood, iron, glass and so on, used in building; and then walls and floors, stairs and windows, formed by the combination of these, would answer to anatomical organs.

Zoölogical Position of Man. External examination of the Human Body shows also that it presents certain resemblances to the bodies of many other animals: head and neck, trunk and limbs, and various minor parts entering into them, are not at all peculiar to it. Closer study and the investigation of internal structure demonstrates further that these resemblances are in many cases not superficial only, but that our Bodies may be regarded as built upon a plan common to them and the bodies of many other creatures: and it soon becomes further apparent that this resemblance is greater between the Human Body and the bodies of ordinary four-footed beasts, than between it and the bodies of birds, reptiles or fishes. Hence, from a zoölogical point of view, man's Body marks him out as belonging to the group of Mammalia (see Zoölogy), which includes all animals in which the female suckles the young; and among mammals the anatomical resemblances are closer and the differences less between man and certain apes than between man and the other mammals; so that zoölogists still, with Linnæus, include man with the monkeys and apes in one subdivision of the Mammalia, known as the *Primates*. That civilized man is mentally far superior to any other animal is no valid objection to such a classification, for zoölogical groups are defined by anatomical and not by physiological characters; and mental traits, since we know that their manifestation depends upon the structural integrity of certain organs, are especially phenomena of function and therefore not available for purposes of zoölogical arrangement.

As man walks erect with head upward, while the great majority of Mammals go on all fours with the head forward and the back upward, and various apes adopt intermediate positions, confusion is apt to arise in considering corresponding parts in man and other animals unless a precise meaning be given to such terms as "anterior" and "posterior." Anatomists, therefore, give those words definite arbitrary significations. The head end is always *anterior* whatever the natural position of the animal, and the opposite end *posterior;* the belly side is spoken of as *ventral,* and the opposite side as *dorsal; right* and *left* of course present no difficulty: the terms *cephalic* and *caudal* as equivalent, respectively, to anterior and posterior, are sometimes used. Moreover, that end of a limb nearer the trunk is spoken of as *proximal* with reference to the other or *distal* end. The words *upper* and *lower* may be conveniently used for the relative position of parts in the natural standing position of the animal.

The Vertebrate Plan of Structure. Neglecting such merely apparent differences as arise from the differences of normal posture above pointed out, we find that man's own zoölogical class, the Mammals, differs very widely in its broad structural plan from the groups including sea-anemones, insects or oysters, but agrees in many points with the groups of fishes, amphibians, reptiles and birds. These four are therefore placed with man and all other Mammals in one great division of the animal kingdom known as the *Vertebrata.* The main anatomical character of all vertebrate animals is the presence in the trunk of the body of two cavities, a dorsal and a ventral, separated by a solid partition; in the adults of nearly all vertebrate animals, a hard axis, the *vertebral column* (*backbone* or *spine*), develops in this partition and forms a central support for the rest of the Body (Fig. 2, *ee*). The dorsal cavity is continued through the neck, when there is one, into the head, and there widens out. Within it are inclosed the chief organs of the nervous system. The bony axis is also continued through the neck and extends into the head in a modified form. The ventral cavity, on the other hand, is confined to the trunk. It contains the main organs connected with the blood-flow together with those of digestion, respiration and excretion.

Upon the ventral side of the head is the *mouth-opening* leading into a tube, the *alimentary canal, f* (Fig. 2), which passes back

through the neck and trunk and opens again on the outside at the posterior part of the latter. In its passage through the trunk-region this canal lies in the ventral cavity.

The Mammalia. In many vertebrate animals the ventral cavity is not subdivided, but in the Mammalia it is; a membranous transverse partition, the *diaphragm* (Fig. 1, *d*), separating it into an anterior *chest* or *thoracic cavity*, and a posterior, or *abdominal cavity*. The alimentary canal and whatever else passes from one of these cavities to the other must therefore perforate the diaphragm.

In the chest, besides part of the alimentary canal, lie important organs, the *heart*, *h*, and *lungs*, *lu* (Fig. 1); the heart being on the ventral side of the alimentary

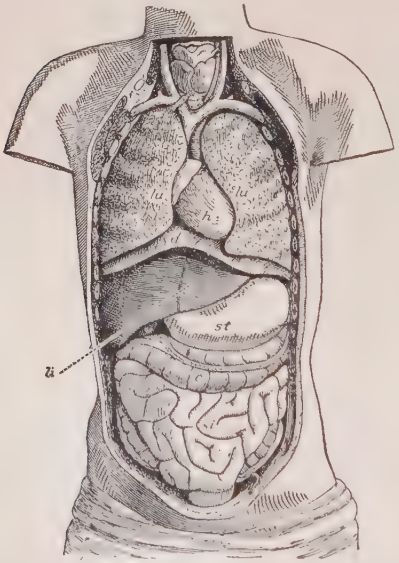


FIG. 1.—Diagram of the Body opened from the front to show the contents of the ventral cavity. *d*, diaphragm; *h*, heart; *lu*, lungs; *st*, stomach; *li*, liver; *si*, small intestines; *c*, large intestine.

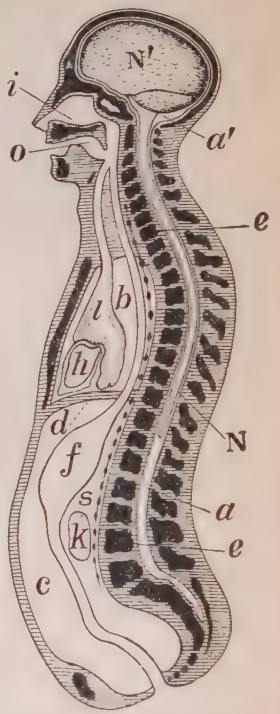


FIG. 2.—Diagrammatic longitudinal section of the Body. *a*, the neural tube, with its upper enlargement in the skull-cavity at *a'*; *N*, the spinal cord; *N'*, the brain; *ee*, vertebræ forming the solid partition between the dorsal and ventral cavities; *b*, the pleural, and *c*, the abdominal division of the ventral cavity, separated from one another by the diaphragm, *d*; *i*, the nasal, and *o*, the mouth chamber, opening behind into the pharynx, from which one tube leads to the lungs, *l*, and another to the stomach, *f*; *h*, the heart; *k*, a kidney; *s*, the sympathetic nervous chain. From the stomach, *f*, the intestinal tube leads through the abdominal cavity to the posterior opening of the alimentary canal.

canal. The abdominal cavity is mainly occupied by the alimentary canal and organs connected with it and concerned in the digestion of food, as the *stomach, st,* the *liver, li,* the *pancreas,* and the small and large intestines, *si* and *c.* Among the other more prominent organs in it are the *kidneys* and the *spleen.*

In the dorsal or neural cavity lie the *brain* and *spinal cord,* the former occupying its anterior enlargement in the head. Brain and spinal cord together form the *cerebrospinal nervous center* commonly called the *central nervous system;* from this spring 43 pairs of nerve trunks, ramifying to all parts of the Body; these make up the *peripheral nervous system* (Fig. 54); in addition there are found in the ventral cavity a number of small nerve-centers united to each other and to the cerebrospinal center by connecting cords, and with their offshoots forming the *sympathetic nervous system.*

The walls of the three main cavities are lined by smooth, moist *serous membranes.* That lining the dorsal cavity is the *arachnoid;* that lining the chest the *pleura;* that lining the abdomen the *peritoneum;* the abdominal cavity is in consequence often called the peritoneal cavity. Externally the walls of these cavities are covered by the *skin,* which consists of two layers: an outer horny layer called the *epidermis,* which is constantly being shed on the surface and renewed from below; and a deeper layer, called the *dermis* and containing blood, which the epidermis does not. Between the skin and the lining serous membranes are *bones, muscles* (the lean of meat), and a great number of other structures which we shall have to consider hereafter. All cavities inside the Body, as the alimentary canal and the air-passages, which open directly or indirectly on the surface are lined by soft and moist prolongations of the skin known as *mucous membranes.* In these two layers are found as in the skin, but the superficial bloodless one is called *epithelium* and the deeper vascular one *corium.*

Diagrammatically we may represent the Human Body in longitudinal section as in Fig. 2, where *aa'* is the dorsal or *neural cavity,* and *b* and *c,* respectively, the thoracic and abdominal subdivisions of the ventral cavity; *d* represents the diaphragm separating them; *ee* is the vertebral column with its modified prolongation into the head beneath the anterior enlargement of the dorsal cavity; *f* is the alimentary canal opening in front through the nose, *i,* and

mouth, *o;* *h* is the heart, *l* a lung, *s* the sympathetic nervous system, and *k* a kidney.

A transverse section through the chest is represented by the diagram Fig. 3, where *x* is the neural canal containing the spinal

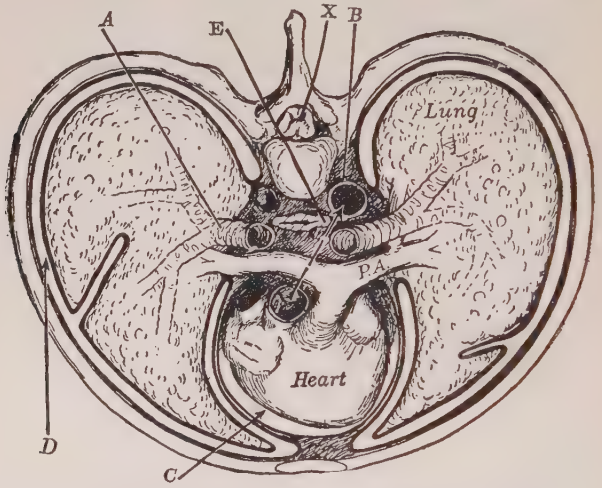


Fig. 3.—Cross-section of thorax. *A*, bronchus, entering the lung; *B*, the aorta cut at its origin and again at the descending part of its arch; *C*, the pericardial space; *D*, the pleural cavity; *E*, the alimentary canal; *P A*, the pulmonary artery; *X*, the neural canal.

cord. In the thoracic cavity are seen the heart, the lungs, part of the alimentary canal, *E;* bronchial tubes, *A*, leading to the lungs; and blood vessels, *B* and *P A*, communicating with the heart; the heavy line on each side covering the inside of the chest-wall and the outside of the lung represents the *pleura.*

Sections through corresponding parts of any other Mammal would agree in all essential points with those represented in Figs. 2 and 3.

The Limbs. The limbs present no such arrangement of cavities on each side of a bony axis as is seen in the trunk. They have an axis formed at different parts of one or more bones (as seen at *U* and *R* in Fig. 4, which represents a cross-section of the forearm near the elbow-joint), but around this are closely-packed soft parts, chiefly muscles, and the whole is enveloped in skin. The only cavities in the limbs are branching tubes which are filled with liquids during life, either *blood* or a watery-looking fluid known as

lymph. These tubes, the *blood* and *lymph-vessels* respectively, are not, however, characteristic of the limbs, for they are present in abundance in the dorsal and ventral cavities and in their walls.

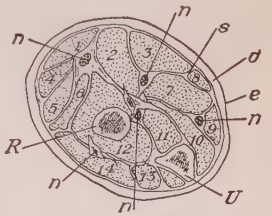


FIG. 4.—A section across the forearm a short distance below the elbow-joint. *R* and *U*, its two supporting bones, the radius and ulna; *e*, the epidermis, and *d*, the dermis of the skin; the latter is continuous below with bands of connective tissue, *s*, which penetrate between and invest the muscles, which are indicated by numbers; *n*, *n*, nerves and vessels.

Microscopic Structure of the Body. For the detailed study of objects too small to be examined with the unaided eye the compound microscope is employed. Important optical conditions for the successful use of this instrument are adequate illumination and sharpness of focus. To secure these in the study of tissues the materials are cut in very thin slices and observed by transmitted light. Viewed thus tissues in their natural state are so nearly transparent that relatively little of their detailed structure can be made out. The practice of histologists, therefore, is first to subject the tissues to the action of preservatives, and then to stain them with suitable dyes. By applying the principle that the different structures of the tissues are likely to differ *chemically* as well as in other respects, dyes can be selected which have greater affinity for some of the chemical components of the tissues than for others. Thus certain of the tissue components will stain with one sort of dye; other components are unaffected by this dye but can be stained with another. This method of *differential staining* enables the various features of tissues to be made clearly visible.

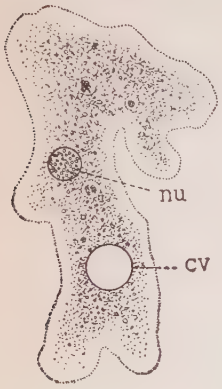


FIG 5.—A simple one-celled organism (Amoeba) exemplifying an unspecialized cell; *nu*, nucleus; *cv*, contractile vacuole (this latter structure is absent from unspecialized cells of higher organisms).

Cells. Examination of the different tissues with the aid of the microscope reveals that they are made up of minute structures, the *cells*. These vary in form and size in different tissues. They are all constructed on a common plan, although in the more highly organized tissues, such as nerves and muscles, this plan is so modified to meet the

special demands of these tissues as not to be easily recognized. A typical unspecialized cell (Fig. 5) consists of a mass of living substance, known as *protoplasm*, of a semi-liquid, gelatinous consistency, about 0.01 millimeter ($\frac{1}{2500}$ inch) in diameter. The protoplasm is usually not perfectly uniform throughout, but shows granules or fine, transparent vesicles through its substance. Imbedded in the protoplasm is a small structure of distinctly different appearance from the rest of the cell. This is the *nucleus*. It presents highly characteristic features which will be studied later. The mass of cell protoplasm outside the nucleus is called *cytoplasm*. This may show a wide range of complexity, from the relatively simple organization indicated in the figure to the complex structure seen in skeletal muscle and nerve cells. Each individual cell is inclosed within an excessively delicate *cell-membrane* consisting of a condensation of the cytoplasm at the cell surface. The membrane has great significance, as pointed out in the next chapter.

Tissues. The individual cells are grouped into masses which are larger or smaller according to the region in which they occur. Obviously only by such a grouping can so large and complex a structure as the Body be built of microscopic units. Any cell mass in which the cells are of one type is called a *tissue*. Thus we speak of muscle tissue or gland tissue according as the cells which make up the tissue in question are muscle cells or gland cells. Many kinds of tissue are widely distributed through the Body, others occur only in special parts. The various tissues will be studied in detail in later chapters.

The tissues with which we are familiar, namely, muscles, skin, heart, and the like, are fairly bulky, so that the extreme tininess of the individual cell units of which they are composed is hard to conceive. It may help some for us to learn that in a cross-section of muscle tissue the size of the shaft of an ordinary pin (one-half square millimeter) there is room for about 200 muscle cells, and in the spaces between the muscle cells room for at least 700 blood-capillaries in addition; the walls of the capillaries being composed, in turn, of excessively thin and delicate cells.

Chemical Composition of the Body. In addition to the study of the Body as composed of tissues and organs which are optically recognizable, we may consider it as composed of a number of

different chemical substances. This branch of knowledge, really presents two classes of problems. On the one hand, we may limit ourselves to the examination of the chemical substances which exist in or may be derived from the dead Body, or, if such a thing were possible, from the living Body entirely at rest; such a study is essentiallly one of structure and may be called *Chemical Anatomy*. But as long as the Body is alive it is the seat of constant chemical transformations in its material, and these are inseparably connected with its functions, the great majority of which are in the long run dependent upon chemical changes. From this point of view, then, the chemical study of the Body presents physiological problems, and might be called *Chemical Physiology*. At present it is customary to include under the term *Biochemistry* the study of the chemical structure of living matter and of the chemical changes occurring in it. At this point we may confine ourselves to the more important substances derived from or known to exist in the Body, leaving questions concerning the chemical changes taking place within it for consideration along with those functions which are performed in connection with them.

Atoms. Modern Physics teaches us that the differences between chemical *elements* are due to differences in the make-up of their atoms. An atom is conceived to consist of a central *nucleus* of incredible minuteness, about which rotate charges of negative electricity, known as *electrons*. The atom as a whole suggests a sort of solar system in which the electrons rotate about the nucleus as planets about the sun. An atom is inconceivably tiny, yet the nucleus and electrons occupy only a small fraction of the whole atomic volume, the remainder being simply the space inside the outermost electronic orbits.

Different elements differ in the make-up of their nuclei, and also in the number and position of the encircling electrons. For our present purpose attention may be concentrated on the latter, which vary from one (in the atom of hydrogen) to ninety-two (in the atom of uranium), and occupy orbits at various definite levels around the nucleus (for departures from this rule see Physics). Each level can contain a certain number of electron-orbits; the inner level has room for only two; the second and third levels for eight each; the fourth and fifth for just eighteen each; and the sixth for thirty-two (a seventh orbit-level is present in the atoms of strongly radio-active elements; see textbooks of Physics or Chemistry). There are theoretically as many different elements as the maximum number of rotating electrons, *i. e.*, 92, each element differing from the one that pre-

cedes it in the series by having one more rotating electron to the atom. All but three of these are actually known. The others probably exist, but have not yet been discovered.

To get some idea of how the atoms unite in forming chemical compounds, which is why this discussion is introduced, two additional facts must be learned: first, that the inner orbit-levels are always filled to capacity before any electrons occur in orbits further out; and second, that the ability of an element to enter into chemical combination depends on the presence of *unoccupied* orbits in its outermost orbit-layer. The dia-

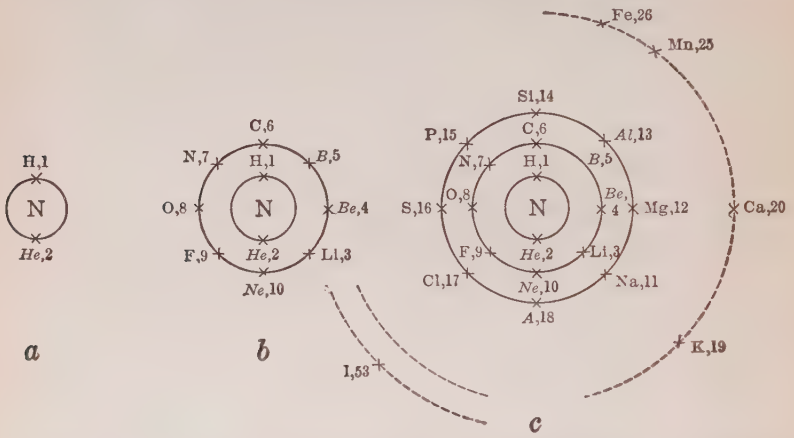


FIG 6.—Diagrams to indicate the numbers of rotating electrons in the atoms of the early part of the atomic series (after Mills). The degree to which the outermost electron orbit is occupied in each element can be deduced from the diagram. *N*, stands for the atomic nucleus. See text for further description.

grams of figure 6 may help to make these points clear. Diagram *a* stands for elements that have rotating electrons in the innermost layer only. Since this layer contains only two orbits there are only two elements in the group; the first, with one rotating electron, is hydrogen; the second, with two, is helium. Hydrogen is very active chemically, as is to be expected from the fact that it has an unoccupied electron-orbit; helium, on the other hand, is completely inert, forming no compounds whatever. In diagram *b* the elements with electrons in the second layer, as well as in the first, are indicated. The number following each chemical symbol gives the number of rotating electrons in the atoms of the element in question. The number ranges from 3 in lithium (Li) to 10 in neon (Ne). All these elements would be expected to be, and are, chemically active except neon, which has no unoccupied electron-orbit. Diagram *c* is a repetition of *b*, extended to include the eight elements with electrons in the third orbit-layer, and also to indicate the numbers and positions of

the four elements in the fourth series that occur in the Body, *i. e.*, potassium, calcium, manganese and iron; and the single element of the fifth series, iodin, that is also present. There is one additional inert element shown in diagram *c*, namely, argon (A) with 18 rotating electrons, and no unoccupied orbit.

Molecules. Atoms that have unoccupied electron-orbits are in a state of tension which causes them to combine with other atoms whenever opportunity offers, thus forming *molecules*. The attraction of atoms for one another is not, however, indiscriminate in the sense in which gravitation is. Most atoms have the power of combining with others precisely like themselves, and will enter this combination unless some other more potent one is at hand, thus giving rise to the diatomic molecules of which most of the elements are composed.

Chemical Compounds. When unlike atoms unite into molecules *chemical compounds* are formed. The main rules governing the union of unlike atoms can be stated simply with reference to diagram *c* of figure 6. The first rule is that elements at the right of the middle vertical line cannot combine directly with each other, but only with elements on the opposite side of the line. The same rule holds for the left side in the main, but not rigidly, for oxygen can combine with nitrogen, phosphorus and sulphur, all of which are near it on the left side of the middle line. (The behavior of elements directly in the middle line will be considered presently.) The second rule is that the elements nearest the inert elements have the lowest "valence," *i. e.*, a valence of one; those in the next position have a valence of two; in the next position a valence of three; and at the most remote position, which is directly opposite the inert elements, a valence of four. (The reader has undoubtedly learned in Chemistry that elements of equal valence combine atom for atom; one atom of a divalent element unites with two univalent atoms; one trivalent atom with three univalent; one quadrivalent with four uni- or two di-valent, etc.)

There are three chemically active elements pictured as being in the middle line directly opposite the inert elements; these require a word of special comment. The first, hydrogen, acts as though it were at the right of the middle line, and in the first position adjoining inert helium, as indeed it is. It is therefore univalent, and able to combine only with elements at the left of the line. Carbon (C) combines about equally well with elements on either side of the line. Silicon (Si) resembles carbon in its main combining properties, but is much less in evidence in the Body.

Elements Composing the Body. Of the 89 elements known to chemists only thirteen enter the composition of the Human Body in any important respect, although four more are usually found

in it in small quantities, making seventeen in all. In the diagrams of figure 6 and in the table on the next page the elements present are in bold faced type, and those absent in italics. It is noteworthy that all the important elements except two are in the first twenty of the atomic series. In other words, the elements associated with life are mainly those with few rather than many rotating electrons.

The table on the next page gives all the elements up to twenty, whether present in the Body or not, with comments on each. From some points of view the elements that are missing are as interesting as those that are present, although this is not the place to discuss the matter. The three elements beyond twenty that are also present are listed at the foot of the table.

1.	**Hydrogen.**	**H.**	One of the four most abundant and important constituents of the Body.
2.	*Helium.*	*He.*	Inert.
3.	**Lithium.**	**Li.**	Found in small quantity; probably not essential.
4.	*Beryllium.*	*Be.*	Absent; occurs sparingly in Nature.
5.	*Boron.*	*B.*	Absent; although abundant in Nature.
6.	**Carbon.**	**C.**	Ranks with hydrogen in abundance and importance; the central element in organic compounds.
7.	**Nitrogen.**	**N.**	Ranks with hydrogen and carbon; the characteristic element of proteins.
8.	**Oxygen.**	**O.**	The most abundant constituent; noteworthy as a factor in oxidation processes.
9.	**Fluorin.**	**F.**	Found in small quantity; probably not essential.
10.	*Neon.*	*Ne.*	Inert.
11.	**Sodium.**	**Na.**	Abundant in inorganic compounds in the Body.
12.	**Magnesium.**	**Mg.**	Less abundant than sodium; occurs in similar situations.
13.	*Aluminum.*	*Al.*	Absent; although very abundant in Nature.
14.	**Silicon.**	**Si.**	Found in small quantity; probably not essential; important in the skeletons of many lower organisms.
15.	**Phosphorus.**	**P.**	An important constituent both of organic and inorganic constituents of the Body.
16.	**Sulphur.**	**S.**	Less abundant than phosphorus; but important.
17.	**Chlorin.**	**Cl.**	An abundant constituent of inorganic compounds in the Body.
18.	*Argon.*	*A.*	Inert.
19.	**Potassium.**	**K.**	Less abundant than sodium; occurs in similar situations.
20.	**Calcium.**	**Ca.**	Occurs abundantly in bones; elsewhere in situations similar to sodium.
25.	**Manganese.**	**Mn.**	Found in small quantity; probably not essential.
26.	**Iron.**	**Fe.**	An essential constituent of special, highly important compounds, blood pigments mainly.
53.	**Iodin.**	**I.**	An essential constituent of special, highly important compounds, thyroid gland extracts.

Inorganic Compounds. These are so called because they occur in non-living as well as in living Nature. The following are the most important that enter into the structure of the Body:

Water; in all the tissues in greater or less proportion and forming about two-thirds of the weight of the whole Body. A man weighing 75 kilos (165 lbs.), if completely dried would therefore lose about 50 kilos (110 lbs.) from the evaporation of water. Of the constituents of the Body the enamel of the teeth contains least water (about 2 per cent), and the saliva most (about 99.5 per cent); between these extremes are all intermediate steps—bones containing about 22 per cent, muscles 75, blood 79.

Water is the medium in which all the active constituents of the body are either dissolved or suspended. It therefore plays a rôle of peculiar importance. In fact, life as we know it on this earth is organized on the basis of water as the all-pervading substance.

Sodium chlorid—Common salt (NaCl); found in all the tissues and liquids; playing various important rôles to be described later.

Calcium phosphate $Ca_3(PO_4)_2$; in the bones and teeth in large quantity; next to water the most abundant inorganic constituent.

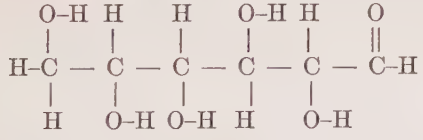
Besides the above, chlorides of potassium, calcium, and ammonium, and carbonates, phosphates, and sulphates of sodium, potassium, ammonium, and magnesium occur in the Body.

Uncombined hydrochloric acid (HCl) is found in the gastric juice.

Organic Compounds. Substances that occur in Nature only in the bodies of living things, or as the result of chemical processes going on in living things, are designated *organic compounds*. Under the same designation come also a great array of substances similar in composition which do not occur naturally, but are made by chemists in their laboratories. Formerly, when much less was known about life-processes than now, it was generally believed that only living things had the power to synthesize organic compounds. We now realize that the chemical processes going on in living organisms obey precisely the same laws as those carried on in test tubes in the laboratory. This discovery, which dates from the synthesis of urea by Wöhler in 1828, is one of the most important in Biology, in that it made men realize that life-processes do not follow special laws of their own, but go on in accordance with the laws of Physics and Chemistry. To the extent to which we can grasp these latter we can make progress in understanding the underlying principles of the life-processes.

Sugar. The first organic compound to be described does not occur in the Body in pure form except in small amounts, but is taken up first because it is the primary organic compound, from which nearly all others are derived, directly or indirectly. Except for a few kinds of bacteria all living things depend for their food, and hence for their life, on the activities of green plants. Green plants contain a particular substance, *chlorophyll,* which enables them to utilize the energy of the sunlight in synthesizing *sugar* out of two simple inorganic substances that are everywhere present in Nature, *water* and *carbon dioxid.* The reaction is written: $6CO_2+6H_2 \rightleftharpoons OC_6H_{12}O_6+6O_2$. Sugar has high energy value; in other words, the energy of sunlight that is locked up in putting the sugar molecules together can be released and made available again by decomposing them. Also it will be noted that sugar contains three of the four elements listed in the table on p. 15 as being especially abundant in the Body. Starting with sugar, then, which provides most of the material needed, and abundant energy as well, it is possible for plants and animals to synthesize the great variety of organic compounds present in the food of Man, and from which, in turn, the constituents of the Body are formed.

The synthesis of sugar from carbon dioxide (CO_2) and water (H_2O) depends on three properties of carbon; two of these have been already mentioned (p. 13); they are quadrivalence, and ability to combine about equally well with such elements as oxygen, nitrogen, and sulphur on the one hand, and hydrogen, sodium, and potassium on the other. A third property, of equal importance, possessed by carbon atoms is that they can join themselves together in long chains, united by one, or in some cases by two, valences, leaving the remaining valences free to attach various atoms at the sides of the carbon chain. The "structural formula" of glucose, given below, illustrates how, as the result of this peculiar



property of carbon, the large and complex molecules of many organic compounds are built up.

There are a great many chemically distinct sugars, of which about a half dozen are of interest in human Physiology. The formula given above applies to the commonly occurring form of *glucose,* which is the primary

sugar. Ordinary table sugar, *sucrose*, and milk sugar, *lactose*, have the formula ($C_{12}H_{22}O_{11}$). These are both directly derived from glucose. Glucose is known as a "monosaccharid," while sucrose and lactose are "disaccharids."

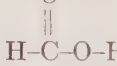
Carbohydrates. The sugars all belong to a chemical class, the *carbohydrates*, which is characterized by having the atoms of hydrogen and oxygen always present in the same proportion as in water. The carbohydrates present in or used by the Body all have the number of carbon atoms six, or a multiple thereof. Beside the sugars these are *glycogen*, *vegetable starch* and *cellulose*.

Glycogen or animal starch ($C_6H_{10}O_5$) is the anhydride of glucose. This is the form in which the excess of sugar is stored in the Body to be drawn upon at need. Glucose is readily converted into it, and it in turn is easily changed back into sugar. In many respects it resembles common vegetable starch. It is present in the muscles of the Body and in the liver, the latter organ alone containing about as much as all the muscles put together.

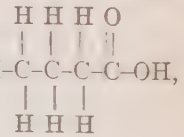
Cellulose, the woody fiber of plants, is not found in the Human Body although a chemically identical substance, tunicin, is found in the bodies of tunicates.

Organic Acids. A grouping of carbon with oxygen and hydrogen of the following form:

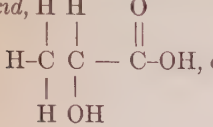
(usually written COOH) is known as a "carboxyl" group. The presence of this group in a molecule makes the latter an *organic acid* (not all organic acids contain this group, although most of them do). The simplest possible acid of this type is formic acid,



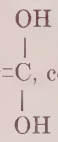
This particular acid is much less important as a bodily constituent than higher related acids in which the H at the left of the C in the formula is replaced by series of carbon atoms of greater or less complexity. In case the spare valences of the carbon atoms are occupied by hydrogen the resulting acids are "fatty acids." *Butyric acid*,



obtained from butter is a good example. *Stearic acid*, an important constituent of animal fat, has eighteen carbon atoms in the chain. In place of one or more of the hydrogens an OH group may be present. *Lactic acid*,



of great importance in muscle Physiology (see Chapter VII) is an example. *Carbonic acid*,



commonly written H_2CO_3, is formed whenever carbon dioxid dissolves in water. Note that all the organic acids described in this paragraph contain only carbon, hydrogen and oxygen. Other acids in which nitrogen is also present are considered below.

Fats. Fats are compounds in which three molecules of fatty acid have reacted with one molecule of glycerol (glycerin) to form large and complex molecules. Glycerol is itself a compound of carbon, hydrogen, and oxygen, so that the molecules of fat contain only these three elements. Two noteworthy facts about fats are: first, that they are insoluble in water, hence have to be handled in the Body, which is a watery organism, in a special manner to be described later; second, that they have weight for weight about twice the energy-value of carbohydrates (see p. 532). The explanation of this high energy-value is found in the smaller relative number of oxygen atoms in the molecules. Energy is derived mainly by oxidation processes, *i. e.*, unions of oxygen with either hydrogen or carbon. To the extent that molecules already contain oxygen their power of yielding energy through oxidation is cut down.

Three fats occur in the Body in large quantities, viz.: *palmatin* ($C_{51}H_{98}O_6$), *stearin* ($C_{51}H_{110}O_6$), and *olein* ($C_{57}H_{104}O_6$). The two former when pure are solid at the temperature of the Body, but in it are mixed with olein (which is liquid) in such proportions as to be kept fluid. The total quantity of fat in the Body is subject to great variations, but its average quantity in a man weighing 75 kilograms (165 pounds) is about 12 kilograms (26.5 pounds).

When a fat is heated with an alkali it is decomposed into its constituent glycerol and fatty acids. The latter combine with the alkali to form *soaps*.

Amino acids. These acids contain nitrogen, and are important because they are the building stones from which *proteins* are constructed. The proteins, in turn, are fundamental constituents of living protoplasm. The simplest amino acids are fatty acids in which one hydrogen is replaced by a so-called *amino group*, $\begin{matrix} H \\ | \\ -N-H \end{matrix}$, commonly written NH_2. A good example is glycocoll (glycin), which is the amino derivative of acetic acid, and has the formula $\begin{matrix} & NH_2 & O \\ & | & \| \\ H-C- & - & C-OH \\ & | & \\ & H & \end{matrix}$, also written CH_2NH_2COOH. Nineteen amino acids have been identified to date, eighteen of which are known to occur in the Body. All amino acids contain carbon, hydrogen, oxygen, and nitrogen; one of them, *cystein*, contains sulphur as well.

Proteins. The amino acids, which are themselves complex substances, are linked together into still more complex protein molecules. It is obvious that with as many as eighteen different acids to combine in different ways and in different proportions a great many different proteins may result. As a matter of fact we have every reason to think that the differences between different kinds of plants and animals are fundamentally chemical differences, and probably due largely, if not wholly, to differences in the proteins of which their bodies are composed. It can be shown mathematically that given as many as eighteen components to put together in various ways even the enormous numbers of kinds of proteins necessary to account for all the species of organisms in existence can easily be attained.

The differences between different sorts of proteins are in some cases very pronounced, so that the chemist would have no difficulty in distinguishing one from the other; in other cases the differences are subtle, revealing themselves only in the peculiar character of the organisms in which they occur. In broad features all the proteins found in living protoplasm are alike; which agrees with the fact that all kinds of protoplasm act more or less similarly.

The common body proteins have a similar percentage composition, falling within the limits given in the following table:

Carbon	50 to 55	per cent.	
Hydrogen	6.5 to 7.3	"	"
Oxygen	19 to 24	"	"
Nitrogen	15 to 17.6	"	"
Sulphur	0.3 to 2.4	"	"

Beside the protein that is part of the living protoplasm animals and particularly plants contain more or less protein material that is either being stored or is part of non-protoplasmic supporting tissues. Bones and gristle, for example, contain proteins that differ from those present in living tissue by lacking one or more amino acids essential to protoplasmic structure. That is why gelatin, made from bones usually, is not an adequate protein food. There are proteins stored in the kernels of wheat and corn that are adequate for ordinary nourishment, but lack a particular amino acid essential for growth.

Conjugated Proteins. In addition to the simple proteins described above there are present in the Body certain groups of compounds consisting of proteins combined with non-protein substances. The most important of these are:

Nucleoproteins, consisting of protein combined with nucleic acid. These are of great interest physiologically since they form the chief constituents of cell nuclei, to which structures are assigned the function of exercising special control over the activities of living cells, and also of being the carriers of hereditary traits.

Glycoproteins, consisting of protein combined with a carbohydrate. **Mucin,** the substance which gives the secretions of the mouth, nose, and throat their peculiar viscous character, is an example of this group.

Phosphoproteins, consisting of protein combined with a phosphorus-containing substance. The **casein** of milk, which forms the curd, is the most familiar member of this group.

Hemoglobins, compounds of protein with a pigment. These are of great physiological importance on account of the property, common to all of them, of acting as transporters of oxygen. The type member of the group, the hemoglobin of Mammalian blood, is of interest chemically on account of the great size of its molecules, which are estimated to contain not less than 2,300 atoms each and to have molecular weight exceeding 16,000.

Nitrogenous Extractives. Under this head are grouped various nitrogen-containing substances most of which represent materials that have done their work in the Body and are about to be got rid of. Nitrogen is present in the living tissues of the Body chiefly

as a part of their proteins. The vital activities of the tissues involve the breaking down of these complex proteins into simpler substances. Part of their carbon combines with oxygen and passes out through the lungs as carbon dioxid; their hydrogen is similarly in large part combined with oxygen and passed out as water; while their nitrogen, with some carbon and hydrogen and oxygen, is passed out in the form of crystalline extractives.

Urea is the most important substance of this class; fully nine-tenths of all the nitrogen eliminated from the Body is in this form. It is a diamide of carbonic acid, having the formula $CO<\begin{matrix}NH_2\\NH_2\end{matrix}$; the relationship of urea to carbonic acid is clear when the formula for the latter is written thus: $CO<\begin{matrix}OH\\OH.\end{matrix}$ Fully 30 grams of urea are eliminated daily from the Body of an adult man.

Creatinine ($C_4H_7N_3O$) is an interesting member of the group of extractives because the amount of it eliminated daily is very constant, regardless of changes in amount of food or exercise taken, and seems to depend closely upon the amount of muscle tissue present in the Body; persons of great muscular development have a larger daily creatinine output than those of smaller build.

Creatine ($C_4H_9N_3O_2$) is closely related chemically to creatinine, but appears to play a very different part in the Body. Creatinine is undoubtedly a waste product of protein decomposition, being merely an incidental product of the vital processes which go on within the organism. Creatine, on the other hand, seems to be an essential constituent of living protoplasm, although just what purpose it serves is not clear. About one per cent of the solid substance of muscle is creatine.

The purin bodies, of which uric acid ($C_5H_4N_4O_3$) is the most familiar example, are derived chiefly, if not wholly, from the decomposition of nucleoproteins and are therefore interesting as being the end products of the vital activities of the cell nuclei.

CHAPTER II

NATURE AND PROPERTIES OF LIVING PROTOPLASM

The Essence of Life. There are a very great number of kinds of living things on the earth, animals and plants, but all of them have certain characteristics in common. The cells of all are composed of *protoplasm*, similar in appearance and in general properties to the protoplasm already described as present in the Body. The one underlying property of living protoplasm, about which all its other properties center, is that of being *self-sustaining;* in other words, of doing spontaneously and aut matically the things that have to be done if life is to continue. Some of these things every cell must do for itself. There are other things that one cell may depend on another to do for it. The things that every cell must do for itself make up what we call the *life-processes.* They actually consist of series of chemical reactions. Protoplasm is so constructed that if the necessary chemical substances are provided, the temperature and water content kept suitable, the waste products of the reactions removed as fast as formed, and no injurious compounds introduced or mistreatment applied, it will go on indefinitely carrying on the chemical reactions that make up the life-processes. The Body as a whole is so organized that through the co-operation of all its parts each cell has these conditions fulfilled more or less successfully; the individual cells are self-sustaining because the Body as a unified organism functions to that end; all the necessary chemical substances are provided and delivered to each cell; suitable temperature and moisture conditions are maintained; the waste products are removed. It is true that a breakdown always occurs sooner or later whereby the Body as a whole meets death; but in the meantime the germinal cells may give rise to a new individual, and so the stream of protoplasm continue uninterrupted. Our main interest in this book is in the processes that go on within the individual cells of the Human Body and in the arrangments that make it possible for these processes to go on. Perpetuation of the race is treated briefly in the chapter on Reproduction.

Metabolism. It has become customary among biologists to designate the sum total of the chemical processes that occur in cells under the term *metabolism.* Some of these processes are absolutely fundamental; in fact make up life itself; the designation *basic metabolism* is applied to these. Others result in growth; these constitute *growth metabolism.* Finally, most kinds of cells perform special functions of one kind or another; the chemical reactions which result in the performance of function make up *functional metabolism.* To illustrate the difference between basic and functional metabolism we may take the familiar example of the biceps muscle of the arm, or any other muscle for that matter. While the muscle is at rest there is no functional metabolism going on in it, since it is not performing any of its special function, which is that of contracting more or less forcibly. It is alive, however, ready to function whenever called upon. The state of being alive implies certain chemical processes in the cells of the muscle, and these processes make up the basic metabolism. The performance of active contraction implies another set of processes, which make up the functional metabolism.

Character of Metabolic Reactions. The chemistry of protoplasm is exceedingly complex, and our knowledge of it is very far from complete. We do have, however, some idea of the kinds of processes going on. We know, for example, that basic metabolism includes a series of reactions in which there is a slow but steady wastage of *proteins* from the cells. We have very little idea what purpose is served by these reactions, but the fact of their occurrence is of fundamental importance in nutrition, since the steady loss of proteins must be made good, or injury and death to the cells will result. Thus proteins are indispensable to proper cell-nourishment. We know, further, that energy-liberation is an important feature of all three types of metabolism; also that the reactions by which the energy is set free are predominantly *oxidations.* In the Body, as in many industrial establishments, needed energy is obtained by the burning of fuel.

In recent years the important discovery has been made that oxidation processes yield energy because they are chemical combinations in which electrons shift from a position of high potential energy to one of lower, and in the shift set energy free. The occurrence of an oxidation implies the interaction of two substances so constituted that as they combine

the requisite electron shift shall occur. An oxidizable fuel (known in modern chemistry as a *reductant*) is a substance that has electrons in position to release energy when opportunity for a suitable electron shift occurs. Any substance that is able to receive electrons into a position of lowered potential energy (known in modern chemistry as an *oxidant*) can serve as the second member of the reacting pair. Oxygen has this ability to a marked degree. In fact the overwhelming majority of all reactions of this type have oxygen as the electron-receiving substance. This is justification for continuing to call these reactions "oxidations," although it is now known that oxygen is only one of many substances able to behave as oxidants.

Physiological Oxidation. Oxygen in molecular state (*i. e.*, atmospheric) functions as an oxidant at ordinary temperatures only with extreme slowness, if at all. In fact, as we all know, to get fuel to burn in ordinary combustion it is necessary to raise the temperature far above the boiling point of water. But physiological oxidations in all higher organisms have to go on at temperatures not exceeding about 45° C. (113° F.). It follows that atmospheric oxygen cannot act directly as oxidant in the Body. We know, however, that in the long run the oxidation processes that go on in us do use atmospheric oxygen; we breathe it in constantly, and exhale compounds of it, *i. e.*, carbon dioxid and water; and if access to it is denied death from suffocation follows promptly. Evidently there is some intermediary substance or substances in the cells by which the utilization of atmospheric oxygen is made possible.

According to the most satisfactory theory yet proposed the process may be pictured somewhat as follows: the fuels burned are sugar or sugar derivatives, composed mainly of carbon, hydrogen and oxygen (p. 17). The theory holds that the fuel molecules unite with water in such a way that all the carbon atoms become combined with oxygen derived from water, with formation of CO_2; this process necessarily leaves the hydrogen that was formerly part of the water in surplus. (For each carbon atom the reaction would be $C+2H_2O=CO_2+4H$.) Thus far the carbon atoms have been serving as reductant and oxygen derived from water as oxidant. In the next stage the hydrogen set free as above acts as reductant and the oxidant is a complex chemical compound present in the cell, which we will call for the moment a "hydrogen

acceptor," because of its ability to unite with hydrogen. Having acted as oxidant and also as hydrogen acceptor and taken up hydrogen, this compound now assumes the function of reductant, and so effectively that it can react with molecular oxygen as oxidant; following this last action the molecules decompose in such a way that the hydrogen previously "accepted" and the oxygen just taken up split off as water, leaving the hydrogen acceptor ready to take up more hydrogen. The final results of the whole process are the using up of fuel and atmospheric oxygen, the setting free of energy, and the formation of carbon dioxid and water. The hydrogen acceptor acts in the long run as "hydrogen transporter," and as such it will be designated hereafter.

Facts About Hydrogen Transporters. The crux of the whole oxidation process in protoplasm according to the above theory, is the alternation of function of the hydrogen transporter between acceptance of hydrogen (oxidant action) and passing the same on to atmospheric oxygen (reductant action). Naturally much attention has been paid to the problem of what substances can function thus, and the question of whether any can be identified in the Body. At present at least three substances are known which appear to act as hydrogen transporters in man and animals. One of these is a normal constituent of most cells; it is known as *glutathione;* the other two belong to a class of substances to be described presently (page 35), under the designation of chemical co-ordinators; these two, *thyroxin* and *adrenin*, carry on their co-ordinating function in whole or part by regulating the *amount of oxidation* in the cells that come under their influence (for further discussion see pp. 216, 528). It is unlikely that the list of hydrogen transporters is exhausted by these three; others may be discovered at any time; meanwhile we have in them an understandable provision whereby essential energy-yielding oxidations can occur in living protoplasm, and incidentally a suggestion as to how the amount of energy made available may be adjusted to the requirements of the organism.

Enzymes. All or nearly all reactions in cells must go on rapidly in order to be serviceable. To insure this, at the relatively low temperatures that prevail, agencies are present that speed up (catalyze) the various reactions. Organic catalyzers are called *enzymes* (formerly ferments). They are known to be colloidal in

structure (see below), and are probably proteins. Their chief characteristics are: *a*, *specificity*, different enzymes are necessary to catalyze different reactions; *b*, *susceptibility to moderate heat*, heating above 60° C. (140° F.) destroys them; *c*, the fact that they are not used up in the reactions, consequently small amounts of enzyme can catalyze their specific reactions in large amount, and for an indefinite time.

Vitamins. In recent years the interesting discovery has been made that metabolism will not go on normally in higher organisms unless they are supplied with small quantities of special chemical substances mostly of plant origin, known as *vitamins*. At least six different vitamins are known to exist; two or three have been prepared in pure or nearly pure state. All we know of the action of individual vitamins is that particular diseases develop when one or another is deficient in the diet. In each case the disease is attributable to a disturbed metabolism. Details are given in Chapter XXV (see also p. 57).

The Organization of Protoplasm. We know that protoplasm consists of seventy-five per cent or more of water in which various molecules are either dissolved or suspended. Among the substances *dissolved* in the water are several inorganic salts and small proportions of sugar and amino acids (see last chapter). The chief materials *suspended* are proteins and complex molecules composed of fats united with phosphoric acid, known as *phosphatides*. Salient characteristics of both proteins and phosphatides are that their molecules are large and irregular in shape. (Although molecules are much too small to be seen, even with highest magnification, it has been possible to obtain quite definite ideas as to their configuration in space.) By the simple physical force of cohesion these large molecules tend to cling together into smaller or larger masses; on account of their irregularity of shape, however, there are numerous interstices among them, which become occupied with molecules of other substances, small enough to enter the spaces, and attracted in their turn by the force of molecular attraction (adhesion). Among the substances thus taken up water and inorganic salts obviously predominate, since they are the substances with small molecules most abundantly represented. We are thus able to think of protoplasm as including in its structure great numbers of tiny aggregates, composed of groups of protein

molecules or phosphatide molecules, or both together, closely intermingled with water and inorganic salts. Each of these aggregates bears an electric charge. Great stress is laid on the existence of ultramicroscopic particles of this sort in protoplasm because it appears that not only the life-processes themselves, but also the performance of special functions on the part of cells, depend on the presence of such particles, and the nature of the performance on the character of the particles and the way in which they interact with one another. A system containing ultramicroscopic particles dispersed in water or some similar medium, is known as a *colloid.*

Surface Energy. The feature of living protoplasm that distinguishes it from dead or dormant protoplasm is its readiness to release energy in the performance of its function whenever occasion arises. To be able to do this it is necessary that the protoplasm have a store of instantly available energy always at hand. This store of energy is thought to be present on the surfaces of the ultramicroscopic particles in the form of *surface energy.* It is a well-known fact of physics that molecules usually attract other molecules like themselves with a different degree of intensity than they do molecules unlike themselves. Protein and phosphatide molecules have a stronger attraction for their own kind than they have for water molecules. It follows that in aggregates of protein or phosphatide molecules those on the surface of the particles are drawn down toward the center of the particles more strongly than they are attracted away from the center by the surrounding water molecules. This one-sided attraction puts the surface molecules under a strain which may serve as a source of energy if it can be utilized.

Basic Metabolism Keeps Surface Energy Available. Just as truly as Nature "abhors a vacuum" it can be said that Nature abhors free energy. No system containing free energy is at rest; it always tends to adjust itself in some way which will reduce the amount of free energy to the minimum. In the case of the surface energy on protoplasmic particles this might be brought about in various ways; the particles might run together into relatively large masses, with a disproportionately great reduction in the surface, and so in the amount of energy. (It can easily be shown that a given mass has a much greater surface when finely subdivided than when in relatively coarse granules); or the particles might attract

to their surfaces enough molecules wandering at large in the surrounding water to use up their unbalanced attractive force (this phenomenon is known as *adsorption*). By one means or another, through the operation of physical forces, the protoplasmic system tends to get rid of its free energy. The best explanation we have for basic metabolism, *i. e.*, for the continuous occurrence of chemical reactions by which energy is continuously supplied, is that the protoplasm is thus kept from settling into a condition of static equilibrium. As fast as free energy disappears the basic metabolism restores it. Protoplasm, even when "at rest," is thus in a state of *dynamic equilibrium;* it is not a fixed unchangeable mass; the presence of innumerable ultramicroscopic particles gives it a gelatinous consistency; but this consistency is not always exactly the same; under certain circumstances one and the same mass of protoplasm may be at one time quite thin and watery, at another time so dense that it could scarcely flow. Changes of this sort usually take place in the course of the performance of function; they imply special chemical activities of one sort or another to be dealt with later.

Cell Membranes. To preserve definite structure in the watery, gelatinous protoplasm individual cells are inclosed in *cell membranes*. These should not be confused with the woody envelopes in which many plant cells are inclosed. Reference here is to the delicate sheaths which surround all cells, both plant and animal, and which serve to keep the semiliquid contents of the cells from running together into a formless mass. The chemical nature of the membranes is not certainly known, although there is reason to believe that they consist of protoplasm condensed at the cell-surface through the operation of definite physical forces, and differing from that of the cells at large chiefly in its greater density. The significance of cell membranes in Physiology lies in part in the fact that all interchanges between living protoplasm and its surroundings must take place through them. Any nourishment any cell receives must pass through the cell membrane before it reaches active protoplasm. Similarly, all materials which cells discharge have to be expelled through the membrane. We shall learn later how much the membranes affect the cells which they inclose through the influence they have on the passage of materials into and out of the cells.

Cell Membranes and Stimulation. Cell membranes have further significance, particularly in the highly specialized cells, muscular, nervous, and glandular (p. 9), in that their condition determines whether these cells shall be functionally active or not. When the membrane is undisturbed it is necessarily in a state of equilibrium with the underlying protoplasm, and so long as this equilibrium persists the only metabolic processes in the protoplasm will be such as occur during "rest." When the condition of the cell membrane is altered, as the result of some energy-change being brought to bear on it, the existing equilibrium is upset, with the result that the processes constituting functional metabolism are set in motion. Any energy-change adequate to alter cell membranes in this manner may serve as a *stimulus*. The activity of the cell which follows automatically on stimulation is its *response to stimulation;* the property of protoplasm by virtue of which response follows stimulation is designated as *irritability*. It should be clear from what has just been said that irritability is not any mysterious "vital phenomenon" but the necessary consequence of the interrelation of cell protoplasm with the cell membrane; in other words, it is inherent in the organization of cells. The present view is that stimulation acts by increasing the *permeability* of the cell membrane, so that some molecules (or ions) ordinarily held within the protoplasm escape when the membrane is altered by stimulation, and in escaping upset the previously existent equilibrium, thus initiating functional activity.

Intercellular Spaces and Intercellular Fluids. In the grouping of cells into tissues (p. 10) we find, even in those that are most compact, minute spaces among the cells. There are points of union between cell and cell, holding the tissue together, but these involve only relatively small portions of the total cell surfaces. Every cell has a large part of its surface fronting on *intercellular spaces*. These spaces are filled with watery fluid called *tissue fluid*, which bathes the individual cells, and, in fact, forms their sole environment. The nourishment of the cells reaches them by way of the tissue fluid; the discharges of waste materials from the cells are into the same. The interchanges between the cells and tissue fluid are therefore the fundamental interchanges of the Body. They are subject, in part, at least, to certain definite laws given below.

Filtration, Osmosis, and Dialysis. At every step in the complex process of supplying the living cells with nourishment and removing from them their harmful waste products the membranes, described above, stand in the way of the substances involved and must be traversed by them. There are membranes between the protoplasm of the cells and the tissue fluid which surrounds them. The digested food must pass through the membranous lining of the digestive tract before it can enter the blood; the oxygen of the air must pass through a membrane in the lungs on its way to the same medium. The juices which are secreted or excreted have to be forced through membranes in passing out from the organs from which they come. The movements of liquids through the membranes of the Body take place for the most part in accordance with certain physical principles which may conveniently be stated at this point.

Filtration. If a membranous bag such as an ox bladder be filled with a liquid and pressure be applied to the liquid in the bag a point may be reached where the liquid is squeezed through the membrane and appears in drops on its outer surface. This is an example of filtration. When a liquid is filtered in this way any undissolved particles or any dissolved substances whose molecules are larger than the interstices of the filter are left behind, but any dissolved substances whose molecules are smaller than the openings in the filter pass through as part of the liquid. Thus a salt solution containing some particles of sand and some molecules of protein might be filtered and the sand and protein removed, but the solution would have just as much salt dissolved in it after filtration as before.

Osmosis. If we should take such a membranous bag as described above filled with salt solution and dip it into a vessel of pure water, so that the surfaces within and without the bag are at the same level, it would be seen after a while that the level of liquid within the bag had risen while that in the vessel outside had correspondingly fallen. That is, there would have been an actual movement of water into the bag with sufficient force to overcome the pressure due to gravity resulting from the change of water level on the two sides of the membrane. *Whenever two solutions of different concentrations are separated by a membrane which is permeable to water there will be a flow of water through the membrane*

in the direction of the greater concentration. This phenomenon is known as *osmosis.* The force which drives the water is called *osmotic pressure* and is said to be exerted by any solution of higher concentration toward any of lower concentration.

Dialysis. A membrane which is permeable to water but not to any particles which may be dissolved in it is known as a semi-permeable membrane; one which allows dissolved substances as well as water to pass is a permeable membrane. Since different substances have different sized molecules it is clear that membranes may be permeable to substances with small molecules without necessarily being permeable to those with large. When two solutions of different concentration are separated by a membrane permeable to one or both of them we have in addition to the movement of water under the driving force of osmotic pressure a movement of dissolved particles through the membrane. This is a special case of the general phenomenon of *diffusion.* Diffusion may be defined as the tendency of substances in solution to distribute themselves evenly throughout the solvent. Where this distribution necessitates the passage of particles through permeable membranes the phenomenon is called *dialysis.* The effect of both osmosis and dialysis is to equalize the concentrations of the solutions on the two sides of the membrane, but it must be remembered that they are entirely distinct phenomena. To illustrate: suppose we have on the two sides of a permeable membrane solutions respectively of sugar and salt of the same concentration, that is, having the same number of particles in solution; there would then be no flow of water in either direction since the osmotic pressure of both solutions is the same, but since neither the sugar nor the salt is evenly distributed throughout the solvent there will be dialysis of both substances until an even distribution is obtained.

Growth Metabolism. During the early years of life all parts of the Body are growing; the total quantity of all the kinds of protoplasm present is increasing more or less continuously. After the adult stage is reached only the outer skin and a few other tissues continue to grow. In addition to the increase in amount of protoplasm, which is the primary feature of growth, there is considerable increase in the bulk of accessory and supporting structures of one kind and another. The manufacture of new

protoplasm involves chemical processes of one sort; the manufacture of accessory tissues processes of quite a different sort. We shall give attention to the latter in the chapters devoted to those tissues. A word will be said here about growth metabolism as applied to protoplasm.

For a long time growth was thought to be merely a phase of ordinary metabolism. We now know that special reactions and specific compounds are involved in the process. About twenty years ago (in 1906 to be exact) the discovery was made that certain cells could be detached from their place in the body of a frog, chick, or other animal to which they belonged, and kept alive indefinitely in glass vessels, provided they were bathed in suitable nutrient media. This discovery enabled many interesting experiments to be tried; among them experiments on the nature of growth. It has been found that cells cannot build new protoplasm directly out of the amino acids, etc., which are brought to them in the tissue fluid in which they are bathed, but must first form intermediate products, known as *trephones*, from which to build the protoplasm. The important point about this is that only certain cells have the power to make trephones, and they are therefore the only ones that can grow wholly by their own efforts. Some other cells may be able to grow and multiply, but only when trephone-forming cells are near at hand to provide them with the necessary supplies of the substance. In early life all cells are able to form trephones; as the adult stage is reached the property is lost by all except certain nucleated blood cells (see p. 315). The result is that the few kinds of cells which continue to grow in the adult are dependent on these blood cells for their trephones. The outer layer of skin grows continuously, but can do so only because its cells are nourished by the blood cells, which produce greater quantities of trephones than their own growth processes require, and so have a surplus on which the cutaneous cells can draw.

Functional Metabolism. Although at first view the Body appears capable of a bewildering variety of activities, the fact is that protoplasm has only three primary functions. Everything we do proves when analyzed to be a manifestation of these three functions, singly or in combination. They are: the making of movements; the reception and transmission of stimuli; and the manu-

facture and outpouring of material. In our Bodies the first is exemplified in muscular action, the second in the functions of sensation and co-ordination as seen in the operation of the sense organs and nervous system, the third in glandular action. Each of these is to be studied in detail in later chapters, and the chemical processes involved will be discussed then. At this point it is important to remind the reader that the importance of functional metabolism, as already stated, is in fulfilling the conditions for making the individual cells self-sustaining. In other words, through the various bodily activities the immediate environment of every cell is kept suitable for its life-processes. Strictly speaking this is one of two results achieved by bodily activity; the second has to do with the preservation of the race, as distinct from the preservation of the individual.

Significance of Functional Metabolism. If we take the liberty of personifying Nature to the extent of ascribing purposes to her, we can say that the "purpose of Nature" with reference to the various species of living beings is to maintain them upon earth from generation to generation. The life of the individual is important only as it serves toward the perpetuation of the race. So long as the good of the individual does not run counter to that of the race the individual is conserved, but as soon as the good of the individual is opposed to that of the race the individual is sacrificed. Thus in a state of nature the old and feeble suffer destruction because their usefulness to the race is over, and they are consuming food which may be required by the young and vigorous. The elaborate humanitarian measures by which civilized men attempt to prevent the destruction of the old, the feeble, and the sick may seem, at first thought, absolutely opposed to the purposes of Nature, and so, perhaps, from a purely physical standpoint they are, but when we recall that the really worth while part of Man's life is intellectual and spiritual rather than physical, and consider the influence of humanitarianism upon this part, we realize that humanitarianism represents, after all, one phase of the highest development of the purpose of Nature with respect to Man.

Through their active functions organisms carry out the "purpose of Nature" with regard to themselves. These functions are peculiarly fitted to enable organisms to maintain themselves and their

race upon earth. Consider, for example, the usefulness of the function of movement, on the one hand, and of sensation and co-ordination on the other. The power of motion is of great advantage to an animal, but only in connection with sensation and co-ordination. The chief usefulness of motion to the organism is the securing of food and the avoidance of harm. Neither of these ends is served by *aimless* motion. To secure food or to avoid harm the organism must have knowledge of its environment. This is gained through the operation of the property of sensation. The mere possession of knowledge is of no avail unless the movements can be directed in accordance with it. For this guidance the property of co-ordination serves.

Only through the successful co-operation of these three functions is the organism able to adapt itself to its environment and so to live. Continued survival requires the continuous co-operation of these functions. The definition sometimes heard of life as *continuous adaptation* emphasizes this truth.

Co-ordination in the Body. The type of co-ordination spoken of above is accomplished through the operation of the nervous system, and is called *nervous co-ordination.* There is another sort of co-ordination which is very important, and of which we shall have much to say, but which is in many respects less familiar in its workings. In the growth process, for instance, co-ordination enters constantly. In most individuals the two legs are the same length, so are the two arms; the ears are about the same size; the eyes are the same color. These things do not happen by accident, but because they are controlled by a definite co-ordinating mechanism. This type of co-ordination differs from that effected through the nervous system chiefly in that it is concerned with processes which go on more slowly. The body carries on this type of co-ordination by means of chemical substances, known as *hormones,* which are manufactured in certain tissues of the body, especially differentiated for that purpose, and conveyed to the tissues upon which they exert their influence through the blood stream. This method of control is called *chemical co-ordination* and shares with *nervous co-ordination* the task of causing the different parts of the exceedingly complex body machine to operate harmoniously.

Emphasis is placed upon the property of co-ordination thus

early in our consideration of the Body because a true appreciation of Physiology requires not only an understanding of the working of the various tissues, but even more a grasp of the manner in which they co-operate to secure that continuous adaptation of the organism to the environment upon which life depends.

CHAPTER III

TISSUES, ORGANS, AND PHYSIOLOGICAL SYSTEMS

Development. Most kinds of animals commence their individual existence as single nucleated cells. The initial cell, known as

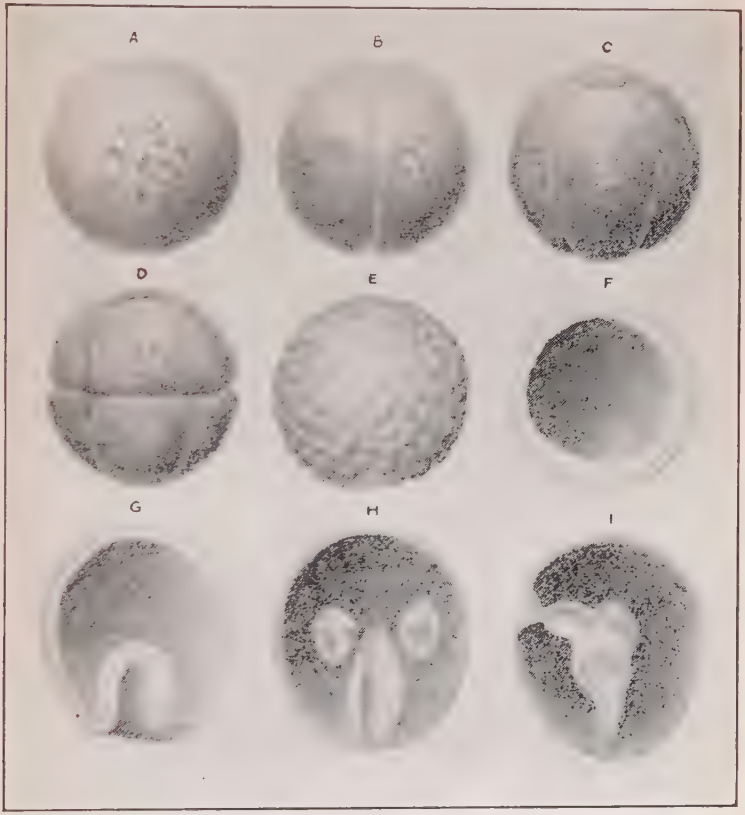


FIG. 7.—Developmental stages, ovum to gastrula (starfish). The first four stages and the end result are essentially similar in man. *A*, ovum; *B*, *C*, *D*, two-, four-, and eight-celled stages. *E*, blastula; *F*, section of same; *G*, early gastrula; *H* and *I*, front and side sections of late gastrula.

the *ovum*, divides by a complex process called *mitosis* (see p. 594) through a two, four, and eight cell stage and then on to form

in the *lower* animals a hollow *blastula* (Fig. 7). As cell division proceeds one wall of the blastula doubles inward (G, Fig. 7) forming a slender sac within the cavity. The embryo is now known as a *gastrula.* Cells detach themselves from the tip of the sac and establish themselves within the cavity of the gastrula. There are thus derived from the single ovum three cell-layers. Development proceeds by continued cell-division until the three primitive layers give rise to all the diverse tissues of which the adult is composed. The outer layer (ectoderm) forms the skin, the sense organs, and the nervous system; the inner layer (endoderm) forms the lining of the digestive tract and the major part of the digestive glands, such as the liver and pancreas; the inner layer (mesoderm) develops into all the other organs, including muscles, blood cells, germ cells, etc.

In man development starts similarly, but instead of a hollow blastula a solid mass of cells, the *morula,* is formed. As this grows the cells in its interior draw apart, giving rise to cavities. The cells also become rearranged into three cell-layers corresponding to those described above; thus a similar structure is attained by a different series of steps.

As the differences in the form and structure of the constituent cells of the embryo become marked, differences in property arise, and it becomes obvious that the whole cell-aggregate is not destined to give rise to a collection of independent living things, but to form a single human being, in whom each part, while maintaining its own life, shall have duties to perform for the good of the whole. In other words, a single *compound individual* is to be built up by the union and co-operation of a number of simple ones represented by the various cells, each of which thenceforth, while primarily looking after its own interests and having its own peculiar faculties, has at the same time its activities subordinated to the good of the entire community.

The Physiological Division of Labor. As the differentiation of tissues proceeds the fundamental physiological properties, originally exhibited in equal degree by all the cells, become distributed among the various tissues. Thus we find certain tissues adapted to execute movements and in these the property of active motion is developed to an especial degree. Other tissues, on the other hand, show little or no active motion but exhibit a marked

degree of conductivity. The higher we look in the animal scale the more marked becomes this division of physiological duties among the tissues. In man it attains its highest development.

Classification of the Tissues. As the Census Report separates the inhabitants of the United States into groups according to various methods of classification, such as ancestry, occupation, and so forth, so we might classify the tissues of the Body according to their ancestry, *i. e.*, the cell-layers from which they are derived, as is done to a slight extent on p. 38, or by selecting the most distinctive properties of each and arranging them into physiological groups; those of each group being characterized by some one prominent function. No such classification can be more than approximately accurate, however, since the same tissue often has more than one well-marked physiological property.

From the facts of functional metabolism given above (p. 33) it is obvious that tissues fall primarily into three main classes, according as they function to perform motions, to receive and transmit stimuli, or to manufacture and pour out material. The first class includes one group only.

1. Motor Tissues. These have the contractility of the original protoplasmic masses highly developed. The most important are the *ciliated cells* and *muscular tissue*. The former line certain surfaces of the Body, and possess on their free surfaces fine threads which are in constant movement. One finds such cells, for example (Fig. 44), lining the inside of the windpipe, where their threads or *cilia* serve, by their motion, to sweep any fluid formed there towards the throat, where it can be coughed up and got rid of. Muscular tissue occurs in three main varieties. One kind is found in the muscles attached to the bones, and is that used in the ordinary voluntary movements of the Body. It is composed of fibers which present cross-stripes when viewed under the microscope (Fig. 40), and is hence known as *striped* or *striated muscular tissue*. Because the muscles which are made of this sort of tissue are attached to bones they are often called *skeletal* muscles. A second kind of muscular tissue is found in the walls of the alimentary canal, the arteries, and some other hollow organs, and consists of elongated cells (Fig. 41) which present no cross-striation. It is known as *smooth* or *unstriated muscular tissue*. The third sort occurs only in the heart. It consists of branched cells presenting

some indications of cross-striation (Fig. 43) and is called *cardiac muscular tissue.*

The second class includes two groups.

2. Receptive Tissues. These include those tissues that are especially susceptible to changes in their surroundings, and are therefore useful in giving to the Body information of what is going on around it. They are largely clustered in the various *sense organs.* The property by virtue of which cells respond to changes in their environment is known as *irritability* or *excitability.* Any change in the environment which serves to arouse response in an excitable tissue constitutes a *stimulus.* All, or nearly all, cells are excitable to some degree or other; the receptive tissues show the property in its state of highest development, and accordingly act as outposts by which the Body keeps in touch with its environment.

3. Conductive Tissues. While most, if not all, of the cells of the Body retain in some degree the ability to transmit stimuli the nervous tissues are specialized to exhibit it in very high degree. They serve, therefore, to bring the various parts of the Body into communication, and particularly to transmit the stimuli impinging on the receptive cells to other, active, tissues where any measures that are called for according to the nature of the stimuli can be set in operation. To fulfill the requirements of nervous coordination certain of the nervous structures have the power to modify the stimuli that pass through them, in ways to be examined in later chapters.

In the class of tissues that manufacture and pour out material are several groups.

4. Supporting Tissues. Including *cartilage* (gristle), *bone,* and *connective tissue.* Of the latter there are several subsidiary varieties, the two more important being *white fibrous connective tissue,* composed mainly of colorless inextensible fibers, and *yellow fibrous tissue,* composed mainly of yellow elastic fibers. All the supporting tissues are used in the Body for mechanical purposes; the bones and cartilages form the hard framework by which softer tissues are supported and protected; and the connective tissues unite the various bones and cartilages, form investing membranes around different organs, and in the form of fine networks penetrate their substance and support their constituent cells. The important fact about these tissues is that their function is not performed by the

living cells scattered among them, but by the non-living products of the activity of these same cells. The function of the cells is that of manufacturing material. The material is strong and heavy, as in bone; moderately flexible, as in cartilage; or fibrous, as in connective tissue. In each case characteristic cells are present to which the true supporting structures owe their existence.

5. Glandular Tissues. In addition to the cells that manufacture supporting structures, the Body contains many masses of cells whose function is to manufacture *special secretions* of one kind or another. These cells are grouped into structures called *glands*. The glandular tissues fall into two main groups. In one group the secretions are poured out to the exterior through *ducts*. The members of this group are referred to as glands of *external secretion;* the salivary, tear, and sweat glands are examples. The members of the second group have no ducts, and pour their secretions directly into the blood. These are glands of *internal secretion* (also commonly spoken of as *endocrine* glands); the thyroid gland in the neck is an example. A great variety of substances are formed by the glands of the Body, serving many useful purposes; details are given in the chapters in which the functions of individual glands are under discussion.

6. Storage Tissues. The Body does not live from hand to mouth: it has always in health a supply of food-materials accumulated in it beyond its immediate needs. This lies in part in the individual cells themselves, but apart from this reserve there are certain cells, which store up considerable quantities of material and constitute what we will call the *storage tissues*. These are especially represented by the liver-cells and fat-cells, which contain in health a reserve fund for the rest of the Body.

7. Protective Tissues. These consist of cells covering the whole exterior of the Body, and of the cells that line the mouth cavity, the bladder, and other spaces that connect directly with the exterior. These cells come in the class of those that manufacture material because some of them (as those in the mouth cavity) manufacture and pour out mucus; others give rise to the hairs and nails, and in other forms to feathers, horns, hoofs, scales, etc. Without the protection afforded by these tissues the Body would be subject to injury at the hands of every trivial contact.

8. Blood-Forming Tissues and Blood Cells. Imbedded in

the spongy interstices of certain bones is a red marrow made up of cells that serve as progenitors for the millions upon millions of cells that float in the blood stream. In spaces in the liver and spleen, and in some other locations in the body, is a tissue (known as *reticulo-endothelial* tissue) related to the red marrow tissue, although serving a somewhat different purpose. The blood cells function mainly by virtue of special substances present within them; they fall, therefore, under the general category of cells whose metabolism has to do with the manufacture of material.

There are a few tissues whose service is largely if not wholly passive.

9. Membranous Tissues. The alimentary tract (stomach and intestines), the air sacs of the lungs, and the small blood vessels are all lined with thin and delicate membranes whose main function is to permit the passage of water or other substances through them. It appears that these membranes may act largely as purely passive agents, through which filtration, osmosis, and dialysis go on. The membranes consist of living cells, however, and it is not certain to what extent they may exercise positive control over the passage of materials through themselves.

There is one class of tissue whose function has to do with racial rather than with individual preservation.

10. The Germinal Tissues. These are concerned in the production of new individuals, and in the Human Body are of two kinds, located in different sexes. The conjunction of the products of each sex is necessary for the origination of offspring, since the female product, egg-cell or ovum, which directly develops into the new human being, remains dormant until it has been *fertilized* and fertilization consists essentially in the fusion of its nucleus with the nucleus of a cell produced by the male.

The Combination of Tissues to Form Organs. The various tissues above enumerated form the building materials of the Body; anatomy is primarily concerned with their structure, and physiology with their properties. If this, however, were the whole matter, the problems of anatomy and physiology would be much simpler than they actually are. The knowledge about the living Body obtained by studying only the forms and functions of the individual tissues would be comparable to that attained about a

great factory by studying separately the boilers, pistons, levers, wheels, etc., found in it, and leaving out of account altogether the way in which these are combined to form various machines; for in the Body the various tissues are for the most part associated to form *organs*, each organ answering to a complex machine like a steam-engine with its numerous constituent parts. And just as in different machines a cogged wheel may perform very different duties, dependent upon the way in which it is connected with other parts, so in the Body any one tissue, although its essential properties are everywhere the same, may by its activity subserve very various uses according to the manner in which it is combined with others. For example: A nerve-fiber uniting the eye with one part of the brain will, by means of its conductivity, when its end in the eye is excited by the irritable tissue attached to it on which light acts, cause changes in the sensory nerve-cells connected with its other end and so arouse a sight sensation; but a similar nerve-fiber running from the brain to the muscles will, also by virtue of its conductivity, when its ending in the brain is excited by a change in a nerve-cell connected with it, stir up the muscle to contract under the control of the will . The different results depend on the different parts connected with the ends of the nerve-fibers in each case, and not on differences in the properties of the nerve-fibers themselves.

It becomes necessary then to study the arrangement and uses of the tissues as combined to form various organs, and this is frequently far more difficult than to make out the structure and properties of the individual tissues. An ordinary muscle, such as one sees in the lean of meat, is a very complex organ, containing not only contractile muscular tissue, but supporting and uniting connective tissue and conductive nerve-fibers, and in addition a complex commissariat arrangement, composed in its turn of several tissues, concerned in the food-supply and waste-removal of the whole muscle. The anatomical study of a muscle has to take into account the arrangement of all these parts within it, and also its connections with other organs of the Body. The physiology of any muscle must take into account the actions of all these parts working together and not merely the functions of the muscular fibres themselves, and has also to make out under what conditions the muscle is excited to activity by changes in other organs, and what changes in these it brings about when it works.

Physiological Systems. Even the study of organs added to that of the separate tissues does not exhaust the matter. In a factory we frequently find machines arranged so that two or more shall work together for the performance of some one work: an electric motor and a loom may, for example, be connected and used together to weave carpets. Similarly in the Body several organs are often arranged to work together so as to attain some one end by their united actions. Such combinations are known as *physiological apparatuses* or *systems*. The circulatory system, for example, consists of various organs (each in turn composed of several tissues) known as heart, arteries, capillaries, and veins. The *heart* forms a force-pump by which the blood is kept flowing through the whole mechanism, and the rest, known together as the *blood vessels*, distribute the blood to the various organs and regulate the supply according to their needs. Again, in the visual apparatus we find the co-operation of (*a*) a set of optical instruments which bring the light proceeding from external objects to a focus upon (*b*) the *retina*, which contains highly irritable parts; these, changed by the light, stimulate (*c*) the *optic nerve*, which is conductive and transmits a disturbance which arouses in turn (*d*) sensory parts in the *brain*. In the production of ordinary sight sensations all these parts are concerned and work together as a visual apparatus. So, too, we find a *respiratory system* consisting primarily of two hollow organs, the *lungs*, which lie in the chest and communicate by the *windpipe* with the back of the throat, from which air enters them. But to complete the respiratory apparatus are many other organs, bones, muscles, nerves, and nerve-centers, which work together to renew the air in the lungs from time to time; and the act of breathing is the final result of the activity of the whole apparatus.

The Relation of Man to His Environment. From infancy the human organism is confronted with the task of maintaining itself alive. To this end all the bodily functions bend themselves. The maintenance of life in man, as in all animals, presents two distinct problems: first, to obtain the necessary food; and second, to cope successfully with the innumerable perils with which the organism is continually confronted. Failure in either of these endeavors means failure in maintaining life itself.

The labor of obtaining food and the struggle to escape harm take

place in the midst of a world filled with creatures engaged in the same labor and the same struggle. Indeed it is the very prevalence of living beings that makes the securing of food labor, and the avoidance of harm a struggle. All the living beings that belong to the animal kingdom are in a more or less continuous state of activity. Each individual, therefore, finds himself surrounded by a continually shifting world of other beings. Nor is inanimate Nature stationary; winds and rains, heat and cold, come and go. To such a constantly changing environment the organism must adapt itself.

In the complex of systems which together make up the Body it is possible to distinguish between those whose immediate function is to maintain the necessary adaptation of the organism to its environment and those which function only indirectly to that end by keeping the Body itself in good working order and each part well supplied with the energy-yielding materials without which activity is impossible. In making such a distinction, however, it must be borne in mind that all the bodily functions work together for the good of the whole Body so that no hard and fast line can be drawn between the two classes of systems. It will be convenient to consider first the systems which are particularly concerned in adapting the Body to its environment.

Adaptive Systems. The Motor System. In all members of the animal kingdom with the exception of certain parasites adaptation is secured mainly through movement. Both for obtaining food and for escaping danger movements either of the whole Body or of parts of it are constantly being resorted to.

In all higher animals the motor mechanism is made up of skeletal muscles, which by their action upon the movable bones of the jointed skeleton bring about the various bodily movements.

There are many types of movement in animals which are not concerned immediately with adaptation to the environment. The movements of breathing, for example, the beat of the heart, and the activities of the stomach. These have to do with maintenance. As emphasized in the last paragraph, however, the classification of systems as adaptive or maintenance is for convenience, and with reference to their most conspicuous functions, and is not to be taken as excluding the systems in one group from having important activities in the other.

The Supporting System. In all but the very simplest animal forms movements are made effective by the action of the muscles upon certain of the supporting tissues. These tissues play, therefore, a very real, although passive part in adaptation. By including the supporting system among the adaptive systems of the Body we emphasize the importance of the supporting structures in making muscular action effective, although here again we must bear in mind that they are also intimately associated with other systems whose chief function is maintenance.

The Receptor System. It is obvious that the Body cannot execute movements adapting it to its surroundings unless it knows what its surroundings are. A blind man, be he never so agile, cannot escape the onward rush of the approaching car while he is ignorant of its coming. He will starve in the midst of abundant food if he does not know where it is to be found.

The Body obtains knowledge of its environment by means of a set of structures known as the sense-organs. In these the property of irritability is developed to a high degree, and so long as they all function properly not much that is important for the organism to know about need escape its knowledge.

The Conductive System. Organs for making movements and organs for receiving impressions from the surroundings are not of themselves adequate to the maintenance of adaptation. It is necessary that the information gained by the sense-organs be transmitted to the muscles so that their movements may correspond to the requirements of the situation. This function is performed by the nervous system. The conduction of stimuli from sense-organs to muscles is not, however, a simple matter. Impressions are continually coming into the Body by way of a number of different channels. Movements must be made not in obedience to any one of these impressions by itself but for the advantage of the whole Body as indicated by all of them taken together. To this end a certain part of the nervous system is adapted for receiving all sorts of incoming stimuli and before passing them on to the motor-organs combining and modifying them to produce the best results.

While for purposes of convenience, the conductive system is classed as one of the adaptive mechanisms, we need to bear in mind that *nervous co-ordination*, for which this system is the agency,

although concerned primarily with direct adaptation, has also much to do with the control of those activities which are primarily concerned with maintenance and only indirectly adaptive.

Maintenance Systems. The systems which are not immediately concerned in the adaptation of the Body to its environment but which serve rather to keep it in proper condition for activity may next be considered.

Activity in the Body involves the manifestation of energy, and in its energy relations the Body is on exactly the same plane as any machine; it is without power to manufacture energy, and must receive whatever energy it obtains from without. The ultimate source of the Body's energy is chemical, being received in the complex substances which serve as food. This energy is made available for the use of the Body chiefly through the process of oxidation. Every living cell in the Body must share in this process, for the energy manifestations of the Body as a whole are simply the sum-total of those of its component cells.

The systems which are concerned with the *maintenance* of *activity* have, then, the task of furnishing to each cell of the Body oxidizable substance and oxygen; they must provide for making good the wear and tear of the cells themselves; and they must remove the waste materials and the excess heat which are formed in connection with the chemical activities of the cells and which would interfere with their proper working if allowed to accumulate.

The Circulatory System consists of the *heart* and *blood-vessels*. It serves to distribute to all the parts of the Body supplies of oxidizable material, of repair material, and of oxygen, and to remove therefrom the accumulated waste products. These functions are accomplished through the agency of a circulating medium, the *blood*.

The Respiratory System consists of the *lungs*, the *bronchial tubes*, and the *trachea*, together with the respiratory muscles. Its function is to bring the outside air to a region where the circulating medium can take up abundant supplies of oxygen, and where it can get rid of those waste products which are in gaseous form.

The Digestive System consists of the alimentary canal and certain associated *glands* (*salivary, liver, pancreas*). It serves to bring the various materials that are taken as food into the forms best adapted for use as repair materials or as oxidizable substance;

when it has so prepared them it turns them over to the circulating medium for distribution.

The Excretory System consists of the *kidney* and *bladder* with their connecting tubes, the *liver*, and the *skin*. It serves to withdraw from the circulating medium and to eliminate from the body those waste products which are in liquid form.

Chemical Co-ordination is secured, as previously stated, by specific *hormones* which govern those bodily activities that are either not readily susceptible to nervous control or in which the best results are secured by supplementing nervous control with chemical. There are special organs, or parts of organs, which manufacture hormones. These are often called *ductless glands*, since they pour their secretions into the blood stream and not by ducts to the surface. They might be grouped together as a system, although nothing would be gained by so doing. Chemical co-ordination plays a part in nearly all forms of bodily activity, and the different hormones will be studied in connection with the activities over which they exert influence.

Through these systems provision is made for the activities of the individual cells. These activities are many and complex. They include oxidative processes, processes involving waste and repair, and doubtlessly many others of which we know nothing. The further study of these cell activities is comprehended under the head of **Metabolism.**

The chemical activities which go on in the cells of the Body give rise to much heat. Some cells generate more heat than others. One of the functions of the circulating medium is to distribute this heat uniformly over the Body. There is constant loss of heat from the surface of the Body. In warm-blooded animals, which have a nearly constant body temperature, the maintenance of balance between heat production and heat loss in the face of constantly varying outside temperatures is a function of great importance. It is studied under the head of **Heat Production** and **Heat Regulation.**

Not immediately concerned with the well-being of the Body itself, but devoted to the well-being of the race as a whole through perpetuating the species is the **Reproductive System.**

Before we turn from this preliminary account of the various systems into which, for convenience, we have grouped the various

bodily structures, we may well emphasize again the *unity of operation* of the Body, so that we shall not fall into the habit of thinking of the different systems as separate mechanisms, operating independently of one another. This unity of operation is well illustrated in one of our commonest everyday experiences, namely, vigorous muscular exercise. Whenever we use our muscles briskly definite activities of the various systems we have classed as *maintenance systems* occur. Thus the heart is thrown into rapid beating; the skin is flushed; the breathing is quickened; the sweat glands are active; if the exercise is prolonged and not too fatiguing, there is likely to be a sharpening of appetite, leading to a greater consumption of food and so to increased digestive activity. All these manifestations accompany muscular exercise, as a matter of course. We shall see later how they are all part of the provision whereby the Body is able to use its muscles effectively. This is but one of many illustrations that might be cited to show the *interdependence* of the various systems. True insight into Human Physiology requires that this interdependence be thoroughly realized.

Animals Compared with Plants. We divide the world of living things into two kingdoms; the plant kingdom and the animal kingdom. The familiar members of the first kingdom seem to us to differ in nearly every important respect from the best known members of the second; an oak tree and a horse are superficially wholly dissimilar. Yet both plants and animals consist of living cells, and the protoplasm of which plant cells are composed is often indistinguishable from that found in animal cells. When we attempt to analyze the difference between plants and animals we find that it cannot be referred to demonstrable difference in the protoplasm. The simplest plants and the simplest animals show the fundamental properties of protoplasm developed in about equal degrees. In fact it is by no means easy always to state positively whether a given one-celled organism should be considered a plant or an animal.

As we go up the scale to the region of higher organization, however, we find no difficulty in deciding whether a living form is plant or animal. The fundamental difference between the higher plants and animals, and the one which involves, as a natural sequence, the superficial differences which are so striking, is a difference in the manner of obtaining nourishment. The higher (green) plants,

as already pointed out, are able to use the energy which falls upon them in the form of sunlight to build up from simple substances present in the air, and in the water to which their roots penetrate, the complex materials of which protoplasm is composed and which, through furnishing the materials needed in metabolism, provide for the carrying on of the necessary activities of living cells. The higher animals, on the other hand, are nourished by means of complex materials which contain within themselves the energy required for the bodily activities. The ultimate source of animal energy, to be sure, is the same as of plant, for the complex materials consumed by animals are derived, directly or indirectly, from plants.

The simple chemical materials needed by plants are very widely distributed, and the sunlight falls, of course, on all parts of the earth. In any location, therefore, that is sufficently suited to plant life to allow the plant to get a start, the chances of being able to continue to live are as good, on the whole, as they would be anywhere. Hence plants do not need to move about. The giant sequoias of the Pacific Slope have lived for centuries upon the spots where they became established as seedlings.

Animals, on the other hand, require materials that are not everywhere present but must be sought in particular places. The successful search for this sort of food involves active motion subject to guidance in accordance with the environment. In a word, *adaptation;* and the presence of mechanisms for adaptation is the most striking feature of the higher animals, just as the presence of a mechanism for utilizing the energy of sunlight is the conspicuous feature of higher plants.

CHAPTER IV

THE SUPPORTING TISSUES

Connective Tissue. This is the most widely distributed of the supporting tissues. It envelopes and pervades all the soft parts of the Body. The various constituents of individual organs are held together by it, and the organs themselves, are supported in their places by the same tissue. Beneath the skin and attaching it rather loosely to the underlying structures is a layer of connective tissue known as the fascia. So completely is the entire Body pervaded by connective tissue that if a solvent could be found which would dissolve away all the tissues of the Body except this one there would still remain in perfect outline not only the whole Body but also each organ down to minutest detail.

This connective tissue framework is commonly called *areolar* tissue. It is composed, in the main, of tough, inelastic strands; these are arranged, however, in most parts of the Body to form a rather loose network, so that in removing the skin from an animal or in separating one muscle from another in making a dissection a blunt instrument readily tears the strands of areolar tissue apart.

The meshes of areolar tissue are everywhere filled with tissue fluid. Thus the various living tissues of the Body, all of which are surrounded by areolar tissue, are nourished.

There are in the Body connective tissue structures in which the individual strands, instead of forming a loose network, are in parallel bundles, forming the toughest and strongest of cords and bands. These are the tendons, by which muscles are attached to bones, and the ligaments which hold the different bones of the skeleton together.

The functional part of connective tissue consists of two sorts of fibers. In most places the white fibers constitute the bulk of the tissue. These are flexible, inelastic strands composed of an albuminoid substance, collagen. The second sort of fibers are the elastic fibers. These are intermingled with the white fibers to some extent in nearly all regions where connective tissue occurs. In certain structures, where a high degree of elasticity is required, elastic fibers make up the entire connective tissue content. Ex-

amples of this sort are the walls of the large arteries and the ligaments connecting the vertebræ. In quadrupeds these fibers form the great ligament which helps to sustain the head (see p. 79). Elastic tissue is yellow in color, and consists chemically of a protein, elastin, which in some important respects differs from the protein of the white fibers.

Connective tissue fibers are not living structures. They owe their origin to certain living cells, the so-called connective tissue cells, which lie irregularly interspersed wherever connective tissue fibers occur (Fig. 8). In areolar tissue many of the cells have

FIG. 8.—Connective tissue cells; *a*, from areolar tissue; *b*, from tendon.

given up their function of forming fibers and have devoted themselves instead to storing within their substance masses of fat. *Adipose* tissue consists of cells of this sort, and occurs in regions where areolar tissue is most abundant, as just under the skin or in masses about certain internal organs.

Temporary and Permanent Cartilages. In early life a great many parts of the supporting framework of the Body, which afterwards become bone, consist of cartilage. Such for example is the case with all the vertebræ, and with the bones of the limbs. In these cartilages subsequently the process known as *ossification* takes place, by which a great portion of the original cartilaginous model is removed and replaced by the true osseous tissue. Often, however, some of the primitive cartilage is left throughout the whole of life at the ends of the bones in joints where it forms the articular cartilages; and in various other places still larger masses remain, such as the costal cartilages, those in the external ears forming their framework, others finishing the skeleton of the nose which is only incompletely bony, and many in internal parts of the Body, as the cartilage of "Adam's apple," which can be felt in the front of the neck, and a number of rings around the windpipe serving to keep it open. These persistent masses are known as the *permanent*, the others as the *temporary cartilages*. In old age many so-called permanent cartilages become *calcified*—that is,

hardened and made unyielding by deposits of lime-salts in them—without assuming the histological character of bone, and this calcification of the permanent cartilages is one chief cause of the want of pliability and suppleness of the frame in advanced life.

Hyaline Cartilage. In its purest form cartilage is flexible and elastic, of a pale bluish-white color when alive and seen in large masses, and cuts readily with a knife. In thin pieces it is quite transparent. Everywhere except in the joints it is invested by a tough adherent membrane, the *perichondrium*.

When a thin slice of hyaline cartilage is examined with a microscope it is found (Fig. 9) to consist of granular nucleated cells, often collected into groups of two, four, or more, scattered through a homogeneous or faintly granular ground-substance or *matrix*. This matrix is composed of protein substances, and owes its origin to the cells imbedded within it. At the time the cartilage was in process of formation these cells laid down the matrix substance in concentric layers about themselves; thus they cut themselves off from each other and from communication with the outside. The substance of the matrix is sufficiently permeable, however, for a certain interchange of food materials between the cartilage cells and the blood, so that the cells are able to remain alive, although their life is naturally an inactive one.

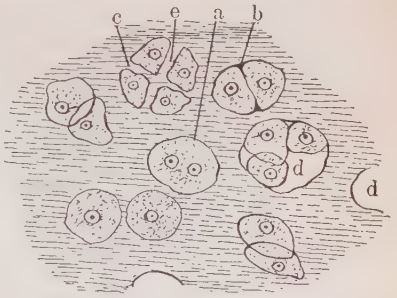


FIG. 9.—A thin slice of cartilage, magnified, to show the cells embedded in the homogeneous matrix. *a*, a cell in which the nucleus has divided; *b*, a cell in which division is just complete; *c*, *e*, a group of four cells resulting from further division of a pair like *b*; the new cells have formed some matrix between them, separating them from another; *d*, *d*, cavities in the matrix from which cells have dropped out during the preparation of the specimen.

All temporary cartilages are of the hyaline type as are also the costal and articular permanent cartilages and the cartilage of the nose and of the windpipe.

Elastic Cartilage is a tissue whose cartilaginous matrix is interwoven with fibers of elastic connective tissue. The result of this interweaving is to give the cartilage a yellow color and a high degree of elasticity. Cartilage of this sort is found in the external ear, the epiglottis, and in certain parts of the larynx.

Fibrocartilage is really a dense fibrous connective tissue within whose spaces a certain amount of matrix material has been deposited. It makes up the intervertebral disks, pads which are interposed between the bones of the vertebral column, and is found also in certain joints, notably the knee-joints and the articulations of the lower jaw.

Bone. The bones which make up the skeleton vary greatly in shape and size, ranging from the long cylindrical bones of the arm and leg to the flat skull bones, and the tiny irregularly shaped ossicles of the middle ear. They all, however, have a similar microscopic structure and similar chemical composition.

The bones may be classified according to their origin as membrane bones or cartilage bones. To the first group belong the flat bones of the skull and the bones of the face (see p. 70). They do not replace cartilage but develop upon a foundation of connective tissue. The so-called cartilage bones replace the temporary cartilages and make up the whole of the bony skeleton, except the membrane bones mentioned above.

The Process of Bone Formation is complicated, and can be described only very briefly here. At the beginning of the development of a membrane bone the strands of connective tissue upon which the bone is to be built become covered with peculiar small cells which are bone-producing cells or *osteoblasts*. These osteoblasts deposit upon the strands whereon they rest protein material which constitutes the organic matrix of bone. There is thus produced a rather open network of bone matrix. By the deposition within the matrix of lime-salts it takes on the character of true bone. The original connective tissue is thus replaced by a network of bony spicules.

The surfaces of this bony mass now become covered with a stout connective tissue membrane, the *periosteum*, whose inner surface is beset with osteoblasts. These deposit upon the underlying mass a layer of compact bone. Thus the fully formed membrane bone consists of outer surfaces of compact bone inclosing a mass of spongy bone.

The replacement of temporary cartilage by bone proceeds from certain points in the cartilage known as centers of ossification. The cartilage itself becomes surrounded by a periosteum like that which incloses membrane bones. At the center of ossification the

osteoblast layer of the periosteum begins to force its way into the cartilage, absorbing much of the latter and leaving only a coarse network, which is presently converted by the osteoblasts into true bone. Meanwhile the periosteum has deposited on the surface of the cartilage a layer of compact bone so that in time the cartilage bone presents a structure not unlike that of membrane bones, a spongy interior inclosed in a layer of compact bone. As the cartilaginous network is being ossified, many osteoblasts are imprisoned within the bony substance. The spaces which they occupy and the tiny canals which radiate therefrom into the bone substances are among the most characteristic appearances of bone viewed under the microscope (Fig. 10).

FIG. 10.—Cross-section of compact bone from the shaft of the humerus. (Sharpey, from Bailey's *Text Book of Histology.*) *a*, space occupied by blood-vessel; *b*, space occupied by osteoblast.

The growth in thickness of bone is accomplished by the addition of layer after layer of compact bone underneath the periosteum. During this process blood vessels of the periosteum often become imbedded within the bony mass. When this occurs the osteoblasts which accompany the blood vessel surround it with concentric layers of bone. In this manner are formed the so-called *Haversian Systems*, each of which consists of the space through which the blood vessel passes with its surrounding rings of bony material.

The increase in length of the long bones is brought about by

plates of cartilage which persist between the shaft of the bone and its extremities. There is a continual growth of bone into these cartilages from both sides, but they grow in thickness with equal rapidity until the adult length of the bone is reached when their growth stops and they are gradually replaced by bone.

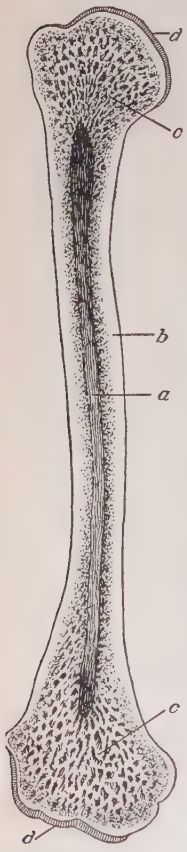


FIG. 11.—The humerus bisected lengthwise. *a*, marrow-cavity; *b*, hard bone; *c*, spongy bone; *d*, articular cartilage.

At the same time that the bone is growing by additions to its outer surfaces a continuous absorption of its inner portions is going on. This absorption is carried on by large, multinuclear cells known as *osteoclasts*. It serves the purpose of preventing the bone from becoming so heavy as to be unmanageable, without sacrificing unduly its strength. As the result of this absorption many adult bones, especially long ones, contain little or no spongy bone except at their ends, the shaft being hollow as shown in Fig. 11.

The Repair of Fractured Bone. When, as happens with unfortunate frequency, a bone is fractured, a sequence of processes is set in motion at the point of injury which results finally in the mending of the break. As an inevitable incident of the injury which causes the fracture there is marked laceration of the periosteum and of the other adjacent tissues. These lacerated tissues pour out a mixture of blood and tissue fluid, known as the *exudate*, which permeates the region of injury. This exudate gradually stiffens until it affords considerable support to the injured bone. Osteoblasts from the inner surface of the periosteum and from the fractured ends of the bone penetrate the exudate. These osteoblasts, little by little, replace the exudate with spongy bone, which holds the injured parts even more firmly in place, and which in turn is gradually replaced by hard bone like that which was present before the injury. The spongy temporary bone is absorbed by the osteoclasts described above.

To secure proper knitting of the fracture two things are of great importance; the first of these is the *reduction* of the fracture, whereby the parts are brought as nearly as possible into their former positions; the second is *immobilization* of the part by means of splints, bandages, or casts to hold the broken ends in place during the formation of the new bony material.

Chemistry of Bone. Bone is composed of inorganic and organic portions intimately combined, so that the smallest distinguishable portion contains both. The inorganic matters form about two-thirds of the total weight of a dried bone, and may be removed by soaking the bone in dilute hydrochloric acid. The organic portion left after this treatment constitutes a flexible mass, retaining the form of the original bone; it consists chiefly of a protein, *ossein*, which by long boiling, especially under pressure at a higher temperature than that at which water boils when exposed freely to the air, is converted into *gelatin*, which dissolves in the hot water. Much of the gelatin of commerce is prepared in this manner by boiling the bones of slaughtered animals, and even well-picked bones may be used to form a good thick soup if boiled under pressure in a Papin's digestor; much nutritious matter being, in the common modes of domestic cooking, thrown away in the bones.

The inorganic salts of bone may be obtained free from organic matter by calcining a bone in a clear fire, which burns away the organic matter. The residue forms a white, very brittle mass, retaining perfectly the shape and structural details of the original bone. It consists mainly of normal calcium phosphate, or *bone-earth* [$Ca_3(PO_4)_2$]; but there is also present a considerable proportion of calcium carbonate ($CaCO_3$) and smaller quantities of other salts.

The Vitamin Factor in Bone Formation. It has long been known that children are likely to suffer from a form of malnutrition in which not enough lime is deposited in the bones to give them the needed strength and rigidity. The disease is known as *rickets* (rachitis). It may develop even when the diet contains abundant lime salts, and also all the phosphoric acid needed for the formation of insoluble calcium phosphate. That cod liver oil is a preventive of and cure for rickets became known some years before the discovery was made that it is rich in a particular vitamin (known as vitamin D) essential for the proper deposition of

lime-salts in the bones. Along with the discovery that cod liver oil contains this essential vitamin the curious observation was being made over and over again that children who play daily in direct sunlight, with no glass intervening, do not develop rickets or get well of it if they have it, without any dosage with cod liver oil at all. The solution to this odd similarity of action of two apparently entirely dissimilar agencies came from the discovery that vitamin D is formed in almost any kind of fat by the action of ultra-violet rays on it. These invisible rays are abundant in sunlight, but are cut off by glass, which is opaque to them. Enough of the ordinary food fats circulate in the blood vessels of the skin so that if the skin is directly exposed to sunlight the vitamin will be formed to a sufficient extent for the bones to deposit their lime normally. Cod liver oil contains the vitamin because the fish either eat food that has been exposed to sunlight, or are themselves exposed to it.

The Relation of Bone Lime to Body Lime. In addition to the great deposits of lime in the bones there are small amounts in all the protoplasmic tissues and in solution in the tissue fluids and blood. Although the lime in the bones is in the form of a hard deposit it is not altogether inaccessible to withdrawal if occasion demands. Such occasion arises if lime is needed for some particular purpose in greater amounts than the diet provides. The best example is in milk-producing animals. Milk always contains a certain definite amount of lime salts, characteristic for the species. If the diet does not furnish enough the bones are depleted of their lime supply to make up the deficit. Nursing mothers very commonly suffer softening of their bones to some extent due to this cause.

A very interesting fact is that the normal balance between bone lime and lime dissolved in the Body fluids is maintained through the action of a particular hormone. This is the first specific instance to be encountered of the chemical co-ordination of bodily processes mentioned on p. 48. The hormone is formed in a special tissue imbedded in the thyroid gland (see p. 214), known as the *parathyroid* tissue. When this tissue produces its hormone, *parathyrin*, at the proper rate the balance between dissolved lime and bone lime is that best suited to bodily welfare. If the hormone is deficient the proportion of lime-salts in the blood is less than normal; if the hormone is overabundant the blood contains more

lime than it should. A deficiency of lime in the blood is apt to be followed by muscular spasms; if the muscles of breathing become involved death from suffocation may ensue. On the other hand, too much lime in the blood may bring on attacks of nausea and vomiting, followed by stupor and in extreme cases death. Why these untoward results should attend shifts in lime content of the blood is unknown. Their existence emphasizes the importance of the hormone by which the balance is ordinarily kept true.

The Size-Regulating Hormone. The size of the Body depends on the size of the skeleton, since the soft tissues cannot do otherwise than adjust themselves to the hard framework of the bones. Some years ago the discovery was made that a peculiar disease, *acromegaly*, in which there is abnormal enlargement of some of the bones, notably of the face and extremities, is associated with overactivity of a mass of tissue at the base of the brain. This tissue mass, the *pituitary body* (Fig. 60), is formed in part by an outgrowth downward from the brain, and in part by an outgrowth upward from the roof of the mouth. The latter portion, known as the *anterior lobe* of the pituitary, and also as the *hypophysis*, appears to be particularly concerned with bony growth. The theory of this control which best explains the known facts is that a hormone is secreted and poured out into the blood which by its presence stimulates growth of the bones. The more abundant the hormone the more vigorous is the growth. The enlargement of the anterior lobe which occurs in acromegaly would account for the occurrence of a more abundant secretion of the hormone. A similar overactivity of the gland appears to characterize the condition of *gigantism*, which gives rise to most of the giants exhibited in side shows. Proof has been obtained recently that in some animals, hence presumably in man as well, the opposite condition, *dwarfishness*, is a result of a deficiency of the pituitary hormone.

We need to bear in mind in discussing hormone action that when an effect is attributed to a hormone we have not offered a complete explanation of it, but only moved the explanation a step farther along. We can say that a man's height is determined by the activity of his pituitary body, but we are still in the dark as to the factors that regulate the latter. Particularly are we ignorant of the manner in which secretion of the hormone is modified when the man has "got his growth."

Hygienic Remarks. Since in the new-born infant many parts which will ultimately become bone consist only of cartilage, the young child requires food which shall contain a large proportion of the lime-salts which are used in building up bone. Nature provides this in the milk, which is rich in such salts (see Chap. XXXIV), and no other food can thoroughly replace it. Long after infancy milk should form a large part of a child's diet. Many children though given food abundant in quantity are really starved, since their food does not contain in sufficient amount the mineral salts requisite for their healthy development.

At birth even those bones of a child which are most ossified are often not continuous masses of osseous tissue. In the large bone of the arm, the humerus, for example, the shaft of the bone is well ossified and so is each end, but between the shafts and each of the articular extremeties there still remains a cartilaginous layer, and at those points the bone increases in length, new cartilage being formed and replaced by bone. The bone increases in thickness by new osseous tissue formed beneath the periosteum. The same thing is true of the bones of the leg. On account of the largely cartilaginous and imperfectly knit state of its bones, it is cruel to encourage a young child to walk beyond its strength, and may lead to "bow-legs" or other permanent distortions. Nevertheless here as elsewhere in the animal body, moderate exercise promotes the growth of the tissues concerned, and it is nearly as bad to wheel a child about forever in a baby-carriage as to force it to overexertion.

The best rule is to let a healthy child use its limbs when it feels inclined, but not by praise or blame to incite it to efforts which are beyond its age, and so sacrifice its healthy growth to the vanity of parent or nurse.

The final knitting together of the bony articular ends with the shaft of many bones takes place only comparatively late in life, and the age at which it occurs varies much in different bones. Generally speaking, a layer of cartilage remains between the shaft and the ends of the bone, until the latter has attained its full adult length. To take a few examples: the lower articular extremity of the humerus only becomes continuous with the shaft by bony tissue in the sixteenth or seventeenth year of life. The upper articular extremity only joins the shaft by bony continuity in the

twentieth year. The upper end of the femur (p. 76) joins the shaft by bone from the seventeenth to the nineteenth year, and the lower end during the twentieth. In the tibia (p. 76) the upper extremity and the shaft unite in the twenty-first year, and the lower end and the shaft in the eighteenth or nineteenth: while in the fibula (p. 76) the upper end joins the shaft in the twenty-fourth year, and the lower end in the twenty-first. The separate vertebræ of the sacrum (p. 75) are only united to form one bone in the twenty-fifth year of life; and the ilium, ischium, and pubis unite to form the *os innominatum* about the same period. Up to about twenty-five then the skeleton is not firmly "knit," and is incapable, without risk of injury, of bearing strains which it might afterwards meet with impunity. To let lads of sixteen or seventeen take exercise in plenty is one thing, and a good one; but to allow them to undergo the severe and prolonged strain of training for and participating in highly organized inter-scholastic football or rowing is quite another, and not devoid of risk.

In early life the bones are less rigid, from the fact that the earthy matters then present in them bear a less proportion to the softer organic parts. Hence the bones of an aged person are more brittle and easily broken than those of a child. The bones of a young child are in fact tolerably flexible and may be distorted by any continued strain; therefore children should never be kept sitting for hours, in school or elsewhere, on a bench which is so high that the feet are not supported. If this be insisted upon (for no child will continue it voluntarily) the thigh-bones will almost certainly be bent over the edge of the seat by the weight of the legs and feet, and a permanent distortion may be produced. For the same reason it is important that a child be made to sit straight while writing, to avoid the risk of producing a lateral curvature of the spinal column. The facility with which the bones may be molded by prolonged pressure in early life is well seen in the distortion of the feet of the Chinese ladies of the old régime, produced by keeping them in tight shoes; and in the extraordinary forms which some races of man produce in their skulls, by tying boards on the heads of the children.

Throughout the whole of life, moreover, the bones remain among the most easily modified parts of the Body; although judging from the fact that dead bones are the most permanent parts of fossil

animals we might be inclined to think otherwise. The living bone, however, is constantly undergoing changes under the influence of the protoplasmic cells imbedded in it, and in the living Body is constantly being absorbed and reconstructed. The experience of physicians shows that any continued pressure, such as that of a tumor, will cause the absorption and disappearance of bone almost quicker than that of any other tissue; and the same is true of any other continued pressure. Moreover, during life the bones are eminently plastic; under abnormal pressures they are found to assume abnormal shapes quickly, being absorbed and disappearing at points where the pressure is most powerful, and increasing at other points.

When a bone is fractured a surgeon should be called in as soon as possible, for once inflammation has set in and the parts have become swollen it is much more difficult to place the broken ends of the bone together in their proper position than before this has occurred. Once the bones are replaced they must be held in position by splints or bandages, or the muscles attached to them will soon displace them again. With rest, in young and healthy persons complete union will commonly occur in three or four weeks; but in old persons the process of healing is slower and is apt to be imperfect.

CHAPTER V

THE SKELETON

Exoskeleton and Endoskeleton. The skeleton of an animal includes all its hard protecting or supporting parts, and is met with in two main forms. One is an *exoskeleton* developed in connection with either the superficial or deeper layer of the skin, and represented by the shell of a clam, the scales of fishes, the horny plates of a turtle, the bony plates of an armadillo, and the feathers of birds. In man the exoskeleton is but slightly developed, but it is represented by the hairs, nails, and teeth; for although the latter lie within the mouth, the study of development shows that they are developed from an offshoot of the skin which grows in and lines the mouth long before birth. Hard parts formed from structures deeper than the skin constitute the *endoskeleton*, which in man is highly developed and consists of a great many *bones* and *cartilages* or gristles, the bones forming the mass of the hard framework of the Body, while the cartilages finish it off at various parts. This framework is what is commonly meant by the skeleton; it primarily supports all the softer parts and is also arranged so as to surround cavities in which delicate organs, as the brain, heart, or spinal cord, may lie with safety. The gross skeleton thus formed is completed and supplemented by another made of the *connective tissues*, which not only, in the shape of tough bands or *ligaments*, tie the bones and cartilages together, but also in various forms pervade the whole Body as a sort of subsidiary skeleton running through all the soft organs and forming networks of fibers around their other constituents; they make, as it were, a microscopic skeleton for the individual modified cells of which the Body is so largely composed, and also form partitions between the muscles, cases for such organs as the liver and kidneys, and sheaths around the blood vessels. The bony cartilaginous framework with its ligaments might be called the skeleton of the organs of the Body, and this finer supporting meshwork the skeleton of the tissues.

The Bony Skeleton (Fig. 12). If the hard framework of the Body were joined together like the joists and beams of a house, the whole mass would be rigid; its parts could not move with relation

to one another, and we should be unable to raise a hand to the mouth or put one foot before another. To allow of mobility the bony skeleton is made of many separate pieces which are joined together, the points of union being called *articulations*, and at many places the bones entering into an articulation are movably hinged together, forming what are known as *joints*. The total number of bones in the Body is more than two hundred in the adult; and the number in children is still greater, for various bones which are distinct in the child (and remain distinct throughout life in many lower animals) grow together so as to form one bone in the full-grown man. The adult bony skeleton may be described as consisting of an *axial skeleton*, found in the head, neck, and trunk; and an *appendicular skeleton*, consisting of the bones in the limbs and in the arches (*u* and *s*, Fig. 12) by which these are carried and attached to the trunk.

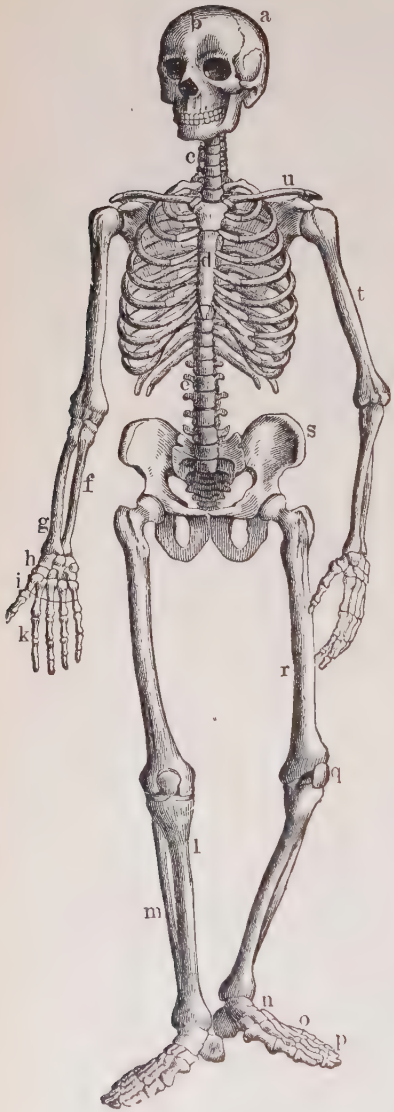


FIG. 12.—The bony and cartilaginous skeleton.

Axial Skeleton. The axial skeleton is made up of the *vertebral column* or *spine*, a side view of which is given in Fig. 13; the *skull*, Fig. 23; the *sternum*, Fig. 26; and the *ribs*, Fig. 28.

The *vertebral column* is the great supporting center for the

whole skeleton and consists of 33 bones grouped as follows from above downward: 7 *cervical*, 12 *dorsal* or *thoracic*, 5 *lumbar*, 5 *sacral*, in the adult united into a single bone, the *sacrum*, and 4 *coccygeal*, or rudimentary tail bones.

The vertebral column occupies the mid-dorsal line of the trunk. On top of it is borne the *skull* (22 bones) made up of two parts; a great box above, composed of 8 bones, which incloses the brain and is called the *cranium;* and a group of 14 bones on the ventral side of this which form the skeleton of the face. Attached by ligaments to the underside of the cranium is the *hyoid bone*, to which the root of the tongue is fixed. There are 12 pairs of *ribs*, attached dorsally to the 12 thoracic vertebræ, one pair to each vertebra. The *sternum*, which occupies the mid-ventral line of the thorax and constitutes the anterior attachment for the ribs is made up of two bones, the *manubrium* and the *body*, and a cartilage, the *ensiform cartilage*.

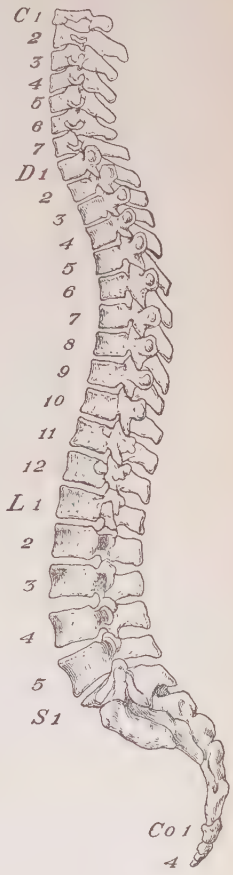


FIG. 13.—Side view of the spinal column. *C* 1–7, cervical; *D* 1–12, dorsal; *L* 1–5, lumbar; *S* 1, sacrum; *Co* 1–4, coccygeal.

Details of the Vertebral Column. The vertebral column is in a man of average height about twenty-eight inches long. Viewed from the side (Fig. 13) it presents four curvatures; one with the convexity forward in the cervical region is followed, in the thoracic, by a curve with its concavity towards the chest. In the lumbar region the curve has again its convexity turned ventrally, while in the sacral and coccygeal regions the reverse is the case. These curvatures give the whole column a good deal of springiness such as would be absent were it a straight rod.

All the vertebræ are built upon the same plan, although with

modifications in various parts of the column. Each consists: 1, of a stout bony body or *centrum* (Fig. 14, *C*), in shape a cylinder flattened at both ends; 2, a bony arch, the *neural arch* (Fig. 14, *A*), attached to the dorsal side of the centrum and inclosing the *neural ring* (Fig. 14, *Fv*). The neural rings of all the vertebræ make up together a long bony tube, the *neural canal*, which contains the spinal cord. Between the bodies of adjoining vertebræ, except in the sacrum and coccyx, are thick pads of elastic cartilage. These permit bending movements which, while quite limited at each

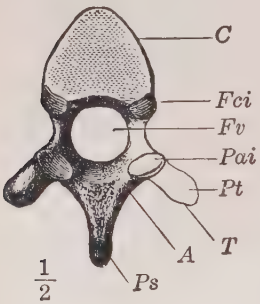


Fig. 14.

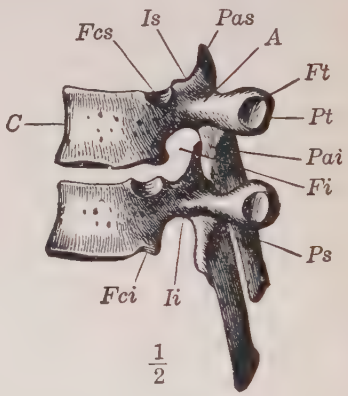


Fig 15.

Fig. 14.—A thoracic vertebra seen from behind, *i. e.*, the end turned from the head.

Fig. 15.—Two thoracic vertebræ viewed from the left side, and in their natural relative positions. *C*, the body; *A*, neural arch; *Ps*, spinous process; *Pas*, anterior articular process; *Pai*, posterior articular process; *Pt*, transverse process; *Ft*, facet for articulation with the tubercle of a rib; *Fcs*, *Fci*, articular surfaces on the centrum for articulation with a rib.

joint may be very considerable in the column as a whole. They also serve to take up a great deal of shock, preventing injury to the Body when one sits down hard or comes down on his heels in walking or jumping. During the hours when one is on his feet these intervertebral pads are packed down by the weight of the Body, and especially by the hammering effect of the movements of walking, running, etc., so that a man may be from a half to three-quarters of an inch shorter at night than he is in the morning. Strong ligaments fasten adjoining vertebræ together; there are also muscles passing from vertebra to vertebra, which by their

contractions assist in bending the body. These muscles are arranged in antagonistic groups; that is, they are so placed that whenever the vertebral column is bent through the contraction of one group the muscles of the antagonistic group are put on the stretch. The neural arch of each vertebra bears a dorsal spinous process (Fig. 14, *Ps*), and a pair of lateral transverse processes (Fig. 14, *Pt*). These serve various purposes; the intervertebral muscles are attached to them; they also bear articular surfaces (*Pas* and *Pai*, Figs. 14 and 15) which sliding upon corresponding surfaces of adjoining vertebræ serve to limit the movements at each joint, and also help to prevent dislocation of the vertebral column. The spinous processes may be felt in the middle of the back. The neural arches are notched (Fig. 15, *Is* and *Fi*), adjoining notches forming rounded openings through which the spinal nerves pass on their way out from the spinal cord.

FIG. 16.

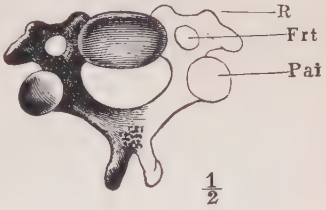


FIG. 17.

FIG. 16.—Diagrammatic representation of a segment of the axial skeleton *V*, a vertebra; *C*, *Cv*, ribs articulating above with the body and transverse process of the vertebra; *S*, the breast-bone. The lighter-shaded part between *S* and *C* is the costal cartilage.

FIG. 17.—A cervical vertebra. *Frt*, vertebral foramen; *Pai*, anterior articular process; *R*, rudimentary rib.

The Cervical Vertebræ (Fig. 17), have rather small bodies and large neural arches; in some of them the spinous process is bifid. They move more freely upon each other than do the vertebræ lower down. A rudimentary rib (*R*, Fig. 17) becomes united early in life to the ventral surface of each transverse process; the foramina (Fig. 17, *Frt*) thus formed give passage to an important artery which ultimately passes into the cranial cavity to carry blood to the brain.

The Atlas and Axis. The first and second cervical vertebræ differ considerably from the rest. The first, or *atlas* (Fig. 18), which carries the head, has a very small body, *Aa*, and a large neural ring. This ring is subdivided by a cord, the *transverse ligament*, *L*, into a dorsal moiety in which the spinal cord lies and a ventral into which the bony process *D* projects. This is the *odontoid process*, and arises from the front of the axis or second cervical vertebra (Fig. 19). Around this peg the atlas rotates

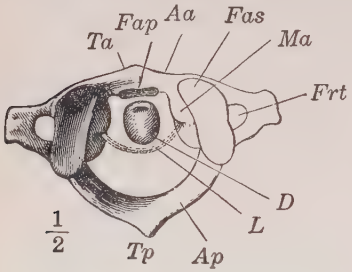


FIG. 18.

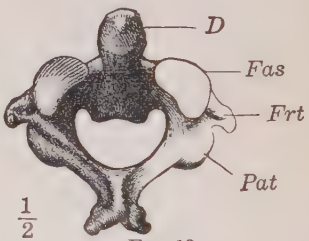


FIG. 19.

FIG. 18.—The *atlas*. FIG. 19.—The *axis*. *Aa*, body of atlas; *D*, odontoid process; *Fas*, facet on front of atlas with which the skull articulates; and in Fig. 19 anterior articular surface of axis; *L*, transverse ligament; *Frt*, vertebral foramen; *Ap*, neural arch; *Tp*, spinous process.

when the head is turned from side to side, carrying the skull (which articulates with the large hollow surfaces *Fas*) with it.

The odontoid process really represents a large piece of the body of the atlas which in early life separates from its own vertebra and becomes united to the axis.

The Thoracic Vertebræ have larger bodies and longer processes than do the cervical vertebræ. They are specially modified for carrying the ribs. Each rib is attached at two points (Fig. 16). The head of the rib fits into an articulation at the junction of two vertebræ, a part of the articular surface being on the centrum of one and a part on the other (Fig. 15, *Fcs* and *Fci*). The second attachment is between a point on the neck of the rib and an articular surface at the end of the transverse process of the posterior of the two vertebræ which the rib touches (Fig. 15, *Ft*).

The Lumbar Vertebræ (Fig. 20) are the largest of all the movable vertebræ and have no ribs attached to them. Their spines

are short and stout and lie in a more horizontal plane than those of the vertebræ in front. The articular and transverse processes are also short and stout.

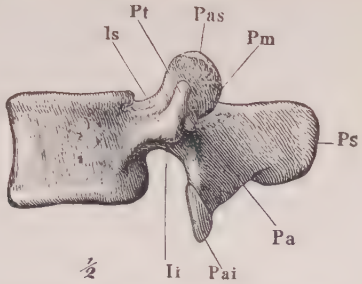


Fig. 20.—A lumbar vertebra, seen from the left side. *Ps*, spinous process; *Pas*, anterior articular process; *Pai*, posterior articular process; *Pt*, transverse process.

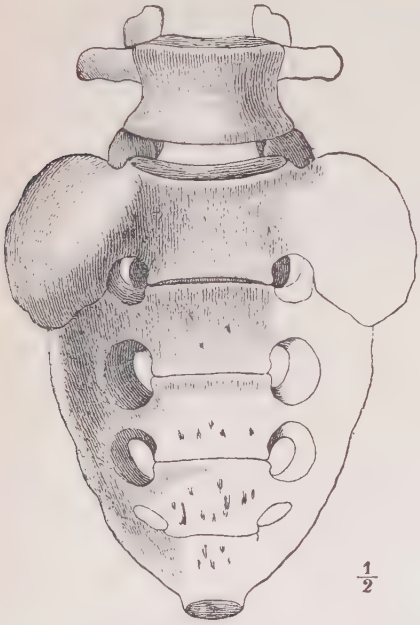


Fig. 22.
The coccyx.

Fig. 21.—The last lumbar vertebra and the sacrum seen from the ventral side.

The Sacrum, which is represented along with the last lumbar vertebra in Fig. 21, consists in the adult of a single bone; but cross-ridges on its ventral surface indicate the limits of the five separate

vertebræ of which it is composed in childhood. It is somewhat triangular in form, its base being directed upwards and articulating with the under surface of the body of the fifth lumbar vertebra. On its sides are large surfaces to which the arch bearing the lower limbs is attached (see Fig. 12). Its ventral surface is concave and smooth and presents four pairs of *anterior sacral foramina*, which communicate with the neural canal. Its dorsal surface, convex and roughened, has four similar pairs of *posterior sacral foramina*.

The *coccyx* (Fig. 22) calls for no special description. The four bones which grow together, or *ankylose*, to form it, represent only the bodies of vertebræ, and even those incompletely.

Details of the Skull. An account of the bones which make up the skull can conveniently be given in tabular form. Examination of the table will show that all the bones are either single or paired. Single bones are all median, paired bones occupy corresponding positions on each side of the mid-line. Figs. 23 and 24 will enable the reader to gain a fairly good notion of the form and relations of individual bones; for greater detail works on anatomy should be consulted.

Cranium:

1 Frontal, forehead (Fig. 23, *F*).
2 Parietal, crown (Fig. 23, *Pr*).
1 Occipital, base of skull (Fig. 23, *O*).
2 Temporal, ear region (Fig. 23, *T*).
1 Sphenoid, base of cranium and back of orbit (Fig. 23, *S*).
1 Ethmoid, between cavities of cranium and nose (Fig. 23, *E*).

Face:

1 Inferior maxilla, lower jaw (Fig. 23, *Md*).
2 Maxillæ, upper jaw, front of hard palate (Fig. 23, *Mx*).
2 Palatine, back of hard palate, front of posterior nares (Fig. 24, *Pt*).
2 Nasal, bridge of nose (Fig. 23, *N*).
1 Vomer, partition between nostrils (Fig. 24, *V*).
2 Inferior turbinate, inside nostrils (not shown in Fig.).
2 Malar, cheeks (Fig. 23, *Z*).
2 Lachrymal, inside wall of orbit (Fig. 23, *L*).

All these bones except the inferior maxilla are immovably joined together in the adult by irregular, saw-tooth like articulations. The inferior maxilla articulates with the temporal bones in such a way as to permit not only rotation about the points of articulation but also a certain amount of sliding from side to side and from back to front, thus making the grinding movements of chewing.

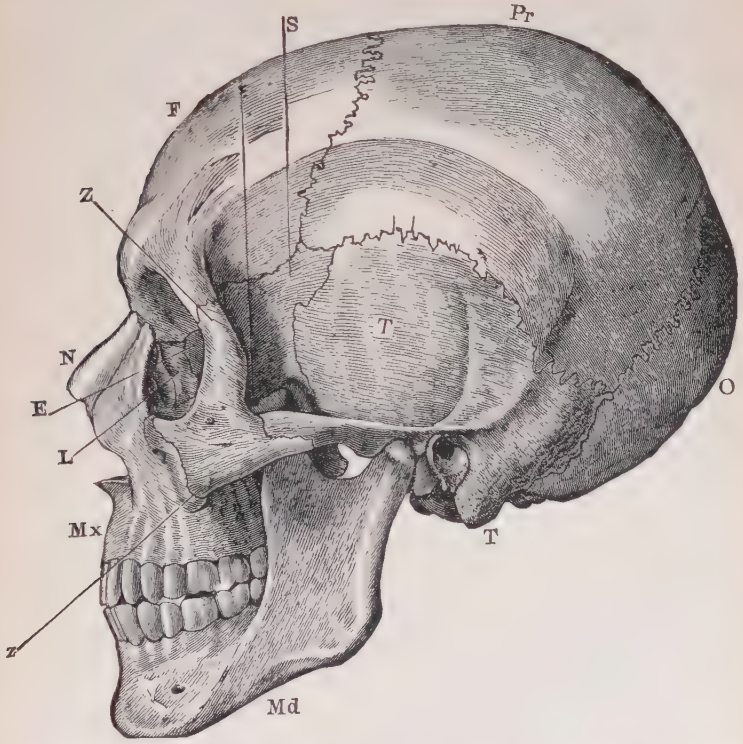


FIG. 23.—A side view of the skull. *O*, occipital bone; *T*, temporal; *Pr*, parietal; *F*, frontal; *S*, sphenoid; *Z*, malar; *Mx*, maxilla; *N*, nasal; *E*, ethmoid; *L*, lachrymal; *Md*, inferior maxilla.

There are several features of the skull which call for special comment. The foramen magnum (Fig. 24) is a large opening into the cranial cavity through the occipital bone; through it the spinal cord passes on its way to the brain. On each side of the foramen magnum is an occipital condyle (Fig. 24, *oc*). These

are the points at which the skull rests upon the atlas. The orbits or eye sockets are outlined in front by the frontal, malars, and maxillæ. The space behind the orbit, between the malar and temporal bones, is occupied by a large muscle which closes the jaw. The shape of the face depends very largely upon the malar bones. The anterior nares, or openings of the nostrils, are bounded by the maxillæ and nasals. The posterior nares, by which the nose communicates with the throat cavity, lie behind the palate bones (Fig. 24). Enlargements of the temporal bones contain the auditory apparatus.

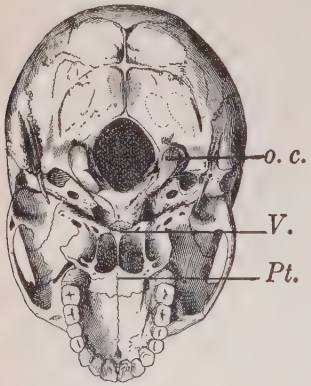


FIG. 24.—The base of the skull. The lower jaw has been removed. At the lower part of the figure is the hard palate forming the roof of the mouth and surrounded by the upper set of teeth. Above this are the paired openings of the posterior nares, and a short way above the middle of the figure is the large median *foramen magnum* with the bony convexities (or *occipital condyles*) *o. c.*, which articulate with the atlas, on its sides; *V*, the vomer; *Pt*, the palatines.

The Hyoid. Besides the cranial and facial bones there is, as already pointed out, one other, the *hyoid* (Fig. 25), which really belongs to the skull, although it lies in the neck. It can be felt in the front of the throat, just above "Adam's apple." The hyoid bone is U-shaped, with its convexity turned ventrally, and consists of a *body* and two pairs of processes called *cornua*. The smaller cornua (Fig. 25, 3) are attached to the base of the skull by long ligaments. The bone serves as an attachment for the base of the tongue. The hyoid is of much interest from the standpoint of comparative anatomy because in the embryonic Human Body it is a part of a structure which corresponds to the gill mechanism of fish, tadpoles, and similar aquatic animals, consisting of several gill arches with gill clefts between them. In the human embryo the gill clefts close before birth, and all the gill arches disappear except those which persist as the hyoid. It is difficult to explain the development and subsequent disappearance of this structure in the embryo except upon the theory which is part of the doctrine of evolution that each

FIG. 25. — The hyoid bone. 1, body; 2, great cornua; 3, small cornua.

individual epitomizes more or less fully in his own developmental history the evolutionary history of the race to which he belongs.

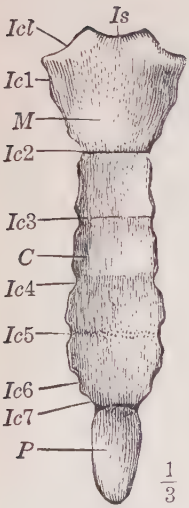


Fig. 26.

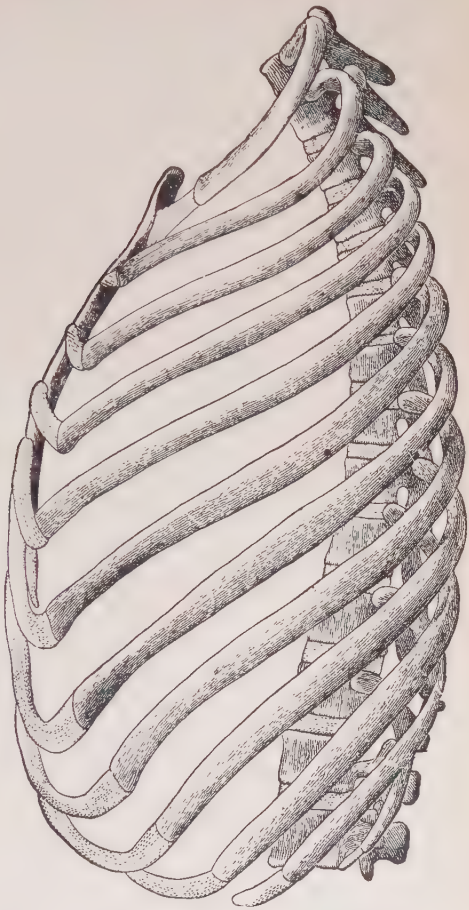


Fig. 27.

Fig. 26.—The sternum seen on its ventral aspect. *M*, manubrium; *C*, body; *P*, ensiform cartilage; *Icl*, notch for the collar-bone; *Ic*, 1–7, notches for the rib-cartilages.

Fig. 27.—The ribs of the left side, with the dorsal and two lumbar vertebræ, the rib-cartilages and the sternum.

The Ribs (Fig. 27). There are twelve pairs of ribs, each being a slender curved bone attached dorsally to the Body and transverse process of a vertebra in the manner already mentioned, and con-

tinued ventrally by a *costal cartilage* (Fig. 16). In the case of the anterior seven pairs, the costal cartilages are attached directly to the sides of the breast-bone; the next three cartilages are each attached to the cartilage of the preceding rib, while the cartilages of the eleventh and twelfth ribs are quite unattached ventrally, so these are called the *free* or *floating ribs*. The convexity of each curved rib is turned outwards so as to give roundness to the sides of the chest and increase its cavity, and each slopes downwards from its vertebral attachment, so that its sternal end is considerably lower than its dorsal.

Sternum. The *sternum* or *breast-bone* (Fig. 26 and Fig. 12) is wider from side to side than dorsoventrally. It consists in the adult of three pieces, and seen from the ventral side has somewhat the form of a dagger. At the upper end are notches for the articulations of the collar-bones (Fig. 26, *Icl*), and along each side notches for the articulations of the anterior costal cartilages (Fig. 26, *Ic*, 1–7).

The Appendicular Skeleton. This consists of the *shoulder-girdle* and the bones of the fore limbs, and the *pelvic girdle* and the bones of the posterior limbs. The two supporting girdles in their natural position with reference to the trunk skeleton are represented in Fig. 28.

The Shoulder-girdle, or Pectoral Arch. This is made up, on each side, of the *scapula* or *shoulder-blade*, and the *clavicle* or collar-bone.

The *scapula* (*S*, Fig. 28) is a flattish triangular bone which can readily be felt on the back of the thorax. It is not directly articulated to the axial skeleton, but lies imbedded in the muscles and other parts outside the ribs on each side of the vertebral column. From its dorsal side arises a crest to which the outer end of the collar-bone is fixed, and on its outer edge is a shallow cup into which the top of the arm-bone fits: this hollow is known as the *glenoid fossa*.

The *collar-bone* (*C*, Fig. 28) is cylindrical and attached at its inner end to the sternum as shown in the figure, fitting into the notch represented at *Icl* in Fig. 26.

The Pelvic Girdle (Fig. 28). This consists of a large bone, the *os innominatum*, *Oc*, on each side, which is firmly fixed dorsally to the sacrum and meets its fellow in the middle ventral line. In the

child each os innominatum consists of three bones, viz., the ilium, the ischium, and pubis. Where these three bones meet and finally ankylose there is a deep socket, the *acetabulum*, into which the head of the thigh-bone fits (see Fig. 12). Between the pubic and ischial bones is the largest foramen in the whole skeleton, known as

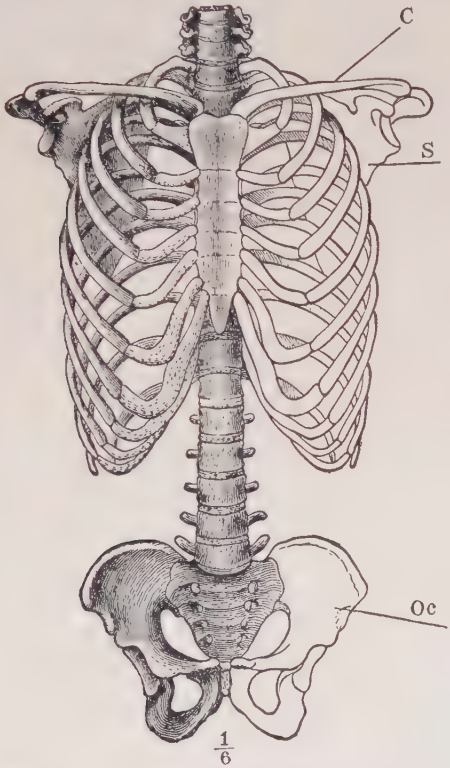


Fig. 28.—The skeleton of the trunk and the limb arches seen from the front. *C*, clavicle; *S*, scapula; *Oc*, innominate bone attached to the side of the sacrum dorsally and meeting its fellow at the *pubic symphysis* in the ventral median line.

the doorlike or *thyroid foramen*. The pubic bone lies above and the ischial below it. The ilium forms the upper expanded portion of the os innominatum to which the line drawn from *Oc* in Fig. 28 points.

Fore and Hind Limbs. Each of these contains thirty bones, and their arrangement is very similar. This is clearly seen in the

figures (29 and 30), and is also brought out in the following table in which the bones of the extremities are enumerated.

	Fore Limb	Hind Limb
a.	Humerus, upper arm.	Femur, thigh.
b.	Ulna, large bone of forearm.	Tibia, shin bone.
c.	Radius, smaller bone of forearm.	Fibula, small bone of calf.
d.	8 carpals, wrist.	7 tarsals, heel and upper instep.
e.	5 metacarpals, hand.	5 metatarsals, lower instep.
f.	14 phalanges, fingers and thumb. (2 in thumb, 3 in each finger).	14 phalanges, toes (2 in great toe, 3 in others).
g.		Patella, kneecap.

FIG. 29.

FIG. 30.

FIG. 29.—The bones of the arm. *a*, humerus; *b*, ulna; *c*, radius; *d*, the carpus; *e*, the fifth metacarpal; *f*, the three phalanges of the fifth digit (*little finger*).

FIG. 30.—Bones of the leg. *a*, femur; *b*, tibia; *c*, fibula; *d*, tarsal bones; *e*, metatarsal bones; *f*, phalanges; *g*, patella.

In general the bones of the hind limb are larger and stronger than the corresponding bones of the fore limb; the femur is the longest bone in the body. The phalanges, however, are smaller in the foot than in the hand. The tarsals are one less in number than the carpals because one of the tarsal bones, the astragalus (Fig. 33, *Ta*), is composed of two bones which have united into one. A structure of the arm corresponding to the patella is the olecranon process of the ulna which can be felt at the back of the elbow; in early life this is a separate bone.

The differences in structure between fore and hind limb correspond to differences of function; the fore limb being a prehensile organ is capable of great freedom of motion; the hind limb, which is a supporting and locomotor organ, is adapted rather to main-

Fig. 31.—Diagram showing the relation of the pectoral arch to the axial skeleton.

tain the weight of the body and to execute the movements of walking and running to advantage. The special adaptation of the arm to its purpose is seen particularly in three things: 1, the comparatively flexible attachment of the pectoral girdle to the axial skeleton (Fig. 31), an attachment composed wholly of muscle and ligament except where the inner ends of the clavicles articulate with the sternum; 2, the rotation of the radius over the ulna, an arrangement which increases very greatly the flexibility of the hand; 3, the articulation of the thumb, which is of such a sort as to allow it to be opposed to any of the fingers, thus enabling the hand to manipulate small objects without difficulty. The leg, on the other hand, is characterized by much greater firmness, which is obtained at the expense of flexibility. The pelvic arch (Figs. 28 and 32) is not only heavy and strong, but is very firmly fixed to

Fig. 32.—Diagram showing the attachment of the pelvic arch to the axial skeleton.

the axial skeleton, the sacrum and os innominatum having a large and strong articulation. The socket into which the head of the femur fits is much deeper than that which receives the head of the humerus, rendering the leg much less liable to dislocation than the arm, but at the same time restricting its movements much more. The foot also in becoming adapted to form a support for the body has sacrificed its prehensible structure almost altogether; the toes are less flexible than the fingers and the great toe cannot be opposed to the others. A special modification of the foot for its particular function is seen in the arching of the instep. As Fig. 33 shows, the bones of the foot form a springy arch, the points of

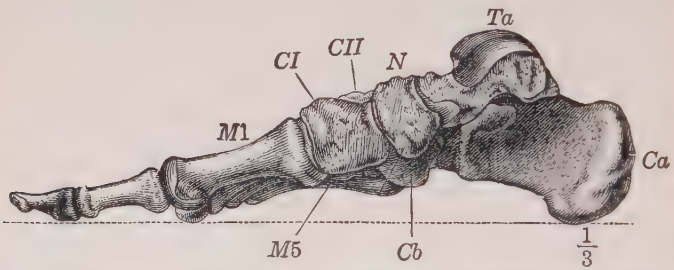


FIG. 33.—The bones of the foot. *Ca*, *calcaneum*, or *os calcis*; *Ta*, articular surface for tibia on the *astragalus*; *N*, scaphoid bone; *CI*, *CII*, first and second cuneiform bones; *Cb*, cuboid bone; *M*1, metatarsal bone of great toe.

contact with the ground being at the extremity of the heel bone (os calcis, *Ca* of figure), and the distal ends of the metatarsals. The bones of the leg are mounted upon the crown of the arch (*Ta* of figure).

Peculiarities of the Human Skeleton. These are largely connected with the division of labor between the fore and hind limbs referred to above, which is carried further in man than in any other creature. Even the highest apes frequently use their fore limbs in locomotion and their hind limbs in prehension, and we find accordingly that anatomically they present less differentiation of hand and foot. The other more important characteristics of the human skeleton are correlated for the most part with the maintenance of the erect posture, which is more complete and habitual in man than in the animals most closely allied to him anatomically. These peculiarities, however, only appear fully in the adult. In the infant the head is proportionately larger, which gives the

center of gravity of the Body a comparatively very high position and renders the maintenance of the erect posture difficult and insecure. The curves of the vertebral column are nearly absent, and the posterior limbs are relatively very short. In all these points the infant approaches more closely than the adult to the ape. The subsequent great relative length of the posterior limbs, which grow disproportionately fast in childhood as compared with the anterior, makes progression on them more rapid by giving a longer stride and at the same time makes it almost impossible to go on "all fours" except by crawling on the hands and knees. In other Primates this disproportion between the anterior and posterior limbs does not occur to nearly the same extent.

In man the skull is nearly balanced on the top of the vertebral column, the occipital condyles which articulate with the atlas being about its middle (Fig. 23), so that but little effort is needed to keep the head erect. In four-footed beasts, on the contrary, the skull is carried on the front end of the horizontal vertebral column and needs special ligaments to sustain it. For instance, in the ox and sheep there is a great elastic cord running from the cervical vertebræ to the back of the skull and helping to hold up the head. Even in the highest apes the skull does not balance on the top of the spinal column; the face part is much heavier than the back, while in man the face parts are relatively smaller and the cranium larger, so that the two nearly equipoise. To keep the head erect and look things straight in the face, "like a man," is for the apes far more fatiguing, and so they cannot long maintain that position. The human spinal column, gradually widening from the neck to the sacrum, is well fitted to sustain the weight of the head, upper limbs, etc., carried by it; and its curvatures, which are peculiarly human, give it considerable elasticity combined with strength. The pelvis, to the sides of which the lower limbs are attached, is proportionately very broad in man, so that the balance can be more readily maintained during lateral bending of the trunk. The arched instep and broad sole of the human foot are also very characteristic. The majority of four-footed beasts, as horses, walk on the tips of their toes and fingers; and those animals, as bears and apes, which like man place the tarsus also on the ground, or in technical language are *plantigrade*, have a much less marked arch there. The vaulted human tarsus, composed of a number of

small bones, each of which can glide a little over its neighbors, but none of which can move much, is admirably calculated to break any jar which might be transmitted to the spinal column by the contact of the sole with the ground at each step. A well-arched instep is therefore rightly considered a beauty; it makes progression easier, and by its springiness gives elasticity to the step.

Articulations. The bones of the skeleton are joined together in very various ways; sometimes so as to admit of no movement at all between them; in other cases so as to permit only a limited range or variety of movement; and elsewhere so as to allow of very free movements in many direction. All kinds of unions between bones are called *articulations*.

Of articulations permitting no movements, those which unite the majority of the cranial bones afford a good example. Except the lower jaw, and certain tiny bones inside the temporal bone belonging to the organ of hearing, all the skull-bones are immovably joined together. This union in most cases occurs by means of toothed edges which fit into one another and form jagged lines of union known as *sutures*. Some of these can be well seen in Fig. 23 between the frontal and parietal bones (*coronal suture*) and between the parietal and occipital bones (*lambdoidal suture*); while another lies along the middle line in the top of the crown between the two parietal bones, and is known as the *sagittal suture*. In newborn children where the sagittal meets the coronal and lambdoidal sutures there are large spaces not yet covered in by the neighboring bones, which subsequently extend over them. These openings are known as *fontanelles*. At them a pulsation can often be felt synchronous with each beat of the heart, which, driving more blood into the brain, distends it and causes it to push out the skin where bone is absent. Another good example of an articulation admitting of no movement is that between the rough surfaces on the sides of the sacrum and the innominate bones.

We find good examples of the second class of articulations—those admitting of a slight amount of movement—in the vertebral column. Between every pair of vertebræ from the second cervical to the sacrum is an elastic pad, the *intervertebral disk*, which adheres by its surfaces to the bodies of the vertebræ between which it lies, and only permits so much movement between them as can be brought about by its own compression or stretching. When

the back-bone is curved to the right, for instance, each of the intervertebral disks is compressed on its right side and stretched a little on its left, and this combination of movements, each individually but slight, gives considerable flexibility to the spinal column as a whole.

Joints. Articulations permitting of movement by the gliding of one bone over another are known as *joints*, and all have the same fundamental structure, although the amount of movement permitted in different joints is very different.

Joint Motions. The wide variety of motions possible to the body group themselves within a small number of classes: *flexion*, the bending of a joint as at elbow or knee; *extension*, the straightening of a joint, the opposite of flexion; *abduction*, the movement of a part away from the axis of the body, as in moving the arm out to the side at right angles, or the thumb and fore finger in spreading the hand; *adduction*, the opposite of abduction; *rotation*, the rolling movement seen when the hand is turned from the palm up to the palm down position, or when one ankle is placed on the opposite knee. There are a few movements, such as the sliding of the jaw from side to side in chewing, that do not fall in any of these classes, but the great majority of joint motions belong either to one of these groups or are combinations of two or more. Thus flexion and abduction of the hip can occur together, or extension and rotation.

Hip-joint. We may take this as a good example of a true joint permitting a great amount and variety of movement. On the os innominatum is the cavity of the *acetabulum* (Fig. 34), which is lined inside by a thin layer of *articular cartilage* which has an extremely smooth surface. The bony cup is also deepened a little by a cartilaginous rim. The proximal end of the femur consists of a nearly spherical smooth *head*, borne on a somewhat narrower *neck*, and fitting into the acetabulum. This head also is covered with articular cartilage; and it rolls in the acetabulum like a ball in a socket. To keep the bones together and limit the amount of movement, *ligaments* pass from one to the other. These are composed of white fibrous connective tissue (Chap. IV) and are extremely pliable, but quite inextensible and very strong and tough. One is the *capsular ligament*, which forms a sort of loose bag all around the joint, and another is the *round ligament*, which passes from the

acetabulum to the head of the femur. Should the latter rotate above a certain extent in its socket, the round ligament and one side of the capsular ligament are put on the stretch, and any further movement which might *dislocate* the femur (that is, remove the head from its socket) is checked. Covering the inside of the capsular ligament and the outside of the round ligament is a layer of flat cells, which are continued in a modified form over the articular cartilages and form the *synovial membrane*. This, which

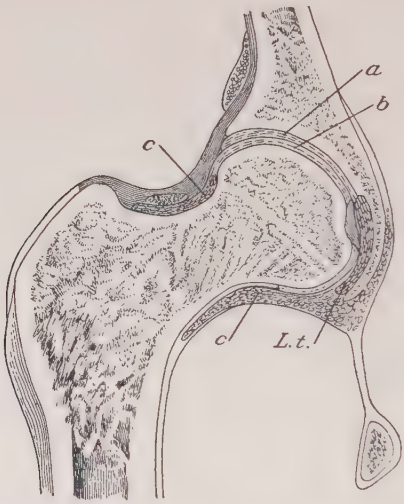


FIG. 34.—Section through the hip-joint. *a* and *b*, articular cartilages; *c*, capsular ligament.

thus forms the lining of the joint, is always moistened in health by a small quantity of glairy *synovial fluid*, something like the white of a raw egg in consistency, and playing the part of the oil with which the contiguous moving surfaces of a machine are moistened; it makes all run smoothly with very little friction.

In the natural state of the parts, the head of the femur and the bottom and sides of the acetabulum lie in close contact, the two synovial membranes rubbing together. This contact is not maintained by the ligaments, which are too loose and serve only to check excessive movement, but by the numerous stout muscles which pass from the thigh to the trunk and bind the two firmly together. Moreover, the atmospheric pressure exerted on the sur-

face of the Body and transmitted through the soft parts to the outside of the air-tight joint helps also to keep the parts in contact. If all the muscles and ligaments around the joint be cut away, it is still found in the dead Body that the head of the femur will be kept in its socket by this pressure, and so firmly as to bear the weight of the whole limb without dislocation, just as the pressure of the air will enable a boy's "sucker" to lift a tolerably heavy stone.

Ball-and-socket Joints. Such a joint as that at the hip is called a ball-and-socket joint and allows of more free movement than any other. Through movements occurring in it the thigh can be *flexed*, or bent so that the knee approaches the chest; or *extended*, that is, moved in the opposite direction. It can be *abducted*, so that the knee moves outwards; and *adducted*, or moved back towards the other knee again. The limb can also by movements at the hip-joint be made to describe a cone of which the base is at the foot and the apex at the hip. Finally, *rotation* can occur in the joint, so that with knee and foot joints held rigid the toes can be turned in or out, to a certain extent, by a rolling around of the femur in its socket.

At the junction of the humerus with the scapula is another ball-and-socket joint permitting all the above movements to even a greater extent. This greater range of motion at the shoulder-joint depends mainly on the shallowness of the glenoid cavity as compared with the acetabulum, and upon the absence of any ligament answering to the round ligament of the hip-joint. Another ball-and-socket joint exists between the carpus and the metacarpal bone of the thumb; and others with the same variety, but a much less range, of movement between each of the remaining metacarpal bones and the proximal phalanx of the finger which articulates with it.

Hinge-joints. Another form of synovial joint is known as a *hinge-joint*. In it the articulating bony surfaces are of such shape as to permit of movement, to and fro, in one plane only, like a door on its hinges. The joints between the phalanges of the fingers are good examples of hinge-joints. If no movement be allowed where the finger joins the palm of the hand it will be found that each can be bent and straightened at its own two joints, but not moved in any other way. The knee is also a hinge-joint, as is the articulation between the lower jaw and the base of the skull which allows

us to open and close our mouths. The latter is, however, not a perfect hinge-joint, since it permits of a small amount of lateral movement such as occurs in chewing, and also of a gliding movement by which the lower jaw can be thrust forward so as to protrude the chin and bring the lower row of teeth outside the upper.

Pivot-joints. In this form one bone rotates around another which remains stationary. We have a good example of it between the first and second cervical vertebræ. The first cervical vertebra or *atlas* (Fig. 18) has a very small body and a very large arch, and its neural canal is subdivided by a transverse ligament (*L*, Fig. 18) into a dorsal and a ventral portion; in the former the spinal cord lies. The second vertebra or *axis* (Fig. 19) has arising from its body the stout bony peg, *D*, called the *odontoid process*. This projects into the ventral portion of the space surrounded by the atlas, and, kept in place there by the transverse ligament, forms a pivot around which the atlas, carrying the skull with it, rotates when we turn the head from side to side. The joints on each side between the atlas and the skull are hinge-joints and permit only the movements of nodding and raising the head. When the head is leaned over to one side, the cervical part of the spinal column is bent.

Another kind of pivot-joint is seen in the forearm. If the limb be held straight out, with the palm up and the elbow resting on the table, so that the shoulder-joint be kept steady while the hand is rotated until its back is turned upwards, it will be found that the radius has partly rolled round the ulna. When the palm is upwards and the thumb outwards, the lower end of the radius can be felt on the outer side of the forearm just above the wrist, and if this be done while the hand is turning over, it will be easily discerned that during the movement this end of the radius, carrying the hand with it, travels around the lower end of the ulna so as to get to its inner side. The relative position of the bones when the palm is upwards is shown at A in Fig. 35, and when the palm is down at B. The former position is known as *supination;* the latter as *pronation*. The elbow end of the humerus (Fig. 35) bears a large articular surface: on the inner two-thirds of this, the ulna fits, and the ridges and grooves of both bones interlocking form a hinge-joint, allowing only of bending or straightening the forearm on the arm. The radius fits on the rounded outer third, and forms

there a ball-and-socket joint at which the movement takes place when the hand is turned from the supine to the prone position; the ulna forming a fixed bar around which the lower end of the radius is moved.

Gliding Joints. These permit as a rule but little movement: examples are found between the closely packed bones of the tarsus and carpus (Figs. 29 and 30), which slide a little over one another when subjected to pressure.

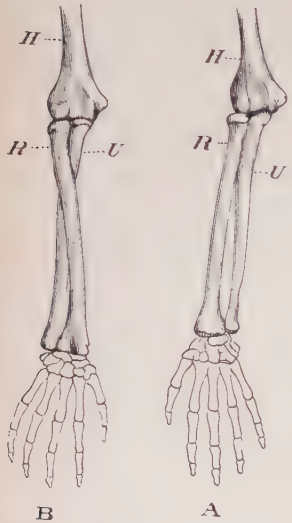


Fig. 35.—A, arm in supination; B, arm in pronation. *H*, humerus: *R*, radius: *U*, ulna.

Hygiene of the Joints. When a bone is displaced or *dislocated* the ligaments around the joint are more or less torn and other soft parts injured. This soon leads to inflammation and swelling which make not only the recognition of the injury but, after diagnosis, the replacement of the bone, or the *reduction of the dislocation*, difficult. Moreover, the muscles attached to it constantly pull on the displaced bone and drag it still farther out of place; so that it is of great importance that a dislocation be reduced as soon as possible. In most cases this can only be attempted with safety by one who knows the form of the bones, and possesses sufficient anatomical knowledge to recognize the direction of the displacement. No injury to a joint should be neglected. Inflammation once started there is often difficult to check and runs on, in a chronic way, until the synovial surfaces are destroyed, and the two bones perhaps grow together, rendering the joint permanently stiff.

Immediate and complete rest has been commonly supposed to be the only proper treatment for sprained joints, but it has been shown recently that massage, properly applied by one expert in its use, has a remarkably beneficial effect upon sprains. Injuries of this sort so severe that under the rest treatment they would require weeks for recovery yield so completely in a few days to massage treatment that the injured individual can participate in

athletic contests. It should be borne in mind that massage to be effective must be applied by an expert in its use.

One articulation that often gives trouble is that between the os innominatum and sacrum, the sacro-iliac junction (Fig. 28). Although this is a large and strong articulation great strain is put upon it, particularly when heavy weights are lifted. Persons who make greater efforts of this sort than their physique justifies often develop severe and persistent back-ache, due to more or less loosening, or even actual displacement, of this articulation. Support by adequate bandaging and complete rest are aids to recovery.

CHAPTER VI

THE STRUCTURE OF THE MOTOR ORGANS

Motion in Animals. Motion is produced in animals by various sorts of motor tissues (p. 39), but in all the underlying mechanical principle is the same, namely, the *forcible contraction* of some element or elements. Various means of making these contractions effective exist in nature. The most familiar is that already cited (p. 45) of causing the contractile structure to pull across a movable joint. In some situations, the human stomach, for example, a hollow organ is completely surrounded by contractile tissues, whose contractions diminish, and whose relaxations permit increase of the capacity of the organ. Still another form of motion is that of the cilia previously mentioned (p. 39).

The Muscles. These are the main motor organs; their general appearance is well known to every one in the lean of butcher's meat. The majority of them being fixed to the skeleton can, by alterations in their form, bring about changes in the form and position of nearly all parts of the Body. With the skeleton and joints, they constitute pre-eminently the organs of motion and locomotion, and are governed by the nervous system which regulates their activity. In fact skeleton, muscles, and nervous system are correlated parts: the degree of usefulness of any one of them largely depends upon the more or less complete development of the others. Man's highly endowed senses and his powers of reflection and reason would be of little use to him, were his muscles less fitted to carry out the dictates of his will or his joints less numerous or mobile. All the muscles are under the control of the nervous system, but all are not governed by it with the co-operation of will or consciousness; some move without our having any direct knowledge of the fact. This is especially the case with certain muscles which are not fixed to the skeleton but surround cavities or tubes in the Body, as the blood vessels and the alimentary canal, and by their movements control the passage of substances through them. The former group, or *skeletal muscles*, are also from their microscopic characters known as *striated muscles*, while the latter, or *visceral*

muscles, are called *unstriated* or *smooth muscles*. The skeletal muscles being generally more or less subject to the control of the will (as for example those moving the limbs) are frequently spoken of as *voluntary*, and the visceral muscles, which change their form independently of the will, as *involuntary*. The heart muscle forms a sort of intermediate link; it is not directly attached to the skeleton, but forms a hollow bag which drives on the blood contained in it and that quite involuntarily; but in its microscopic structure it resembles somewhat the skeletal voluntary muscles. The muscles of respiration are striated skeletal muscles and, as we all know, are to a certain extent subject to the will; any one can draw a deep breath when he chooses. But in ordinary quiet breathing we are quite unconscious of their working, and even when attention is turned to them the power of control is limited; no one can voluntarily hold his breath long enough to suffocate himself. As we shall see hereafter, moreover, any one or all of the striated muscles of the Body may be thrown into activity independently of or even against the will, as, to cite no other instances, is seen in the "fidgets" of nervousness and the irrepressible trembling of extreme terror; so that the names voluntary and involuntary are not good ones, but so far as we use them they indicate no more than the general fact that the skeletal muscles are as a group responsive to the will while the smooth muscles are not.

The Skeletal Muscles. In its simplest form a skeletal muscle consists of a red soft central part, the *belly*, which tapers at each end and there passes into one or more dense white cords which consist almost entirely of white fibrous connective tissue. These terminal cords are called the *tendons* of the muscle and serve to attach it to parts of the skeleton. In Fig. 36 is shown the *biceps muscle* of the arm, which lies in front of the *humerus*. Its fleshy belly is seen to divide above and end there in two tendons, one of which, *Bl*, is fixed to the scapula, while the other, *Bb*, joins the tendon of a neighboring muscle (the *coraco-brachial*, *Cb*), and is also fixed above to the shoulder-blade. Near the elbow-joint the muscle is continued into a single tendon, *B'*, which is fixed to the radius, but gives an offshoot, *B''*, to the connective-tissue membranes lying around the elbow-joint.

The belly of every muscle possesses the power of shortening forcibly under certain conditions. In so doing it pulls upon the

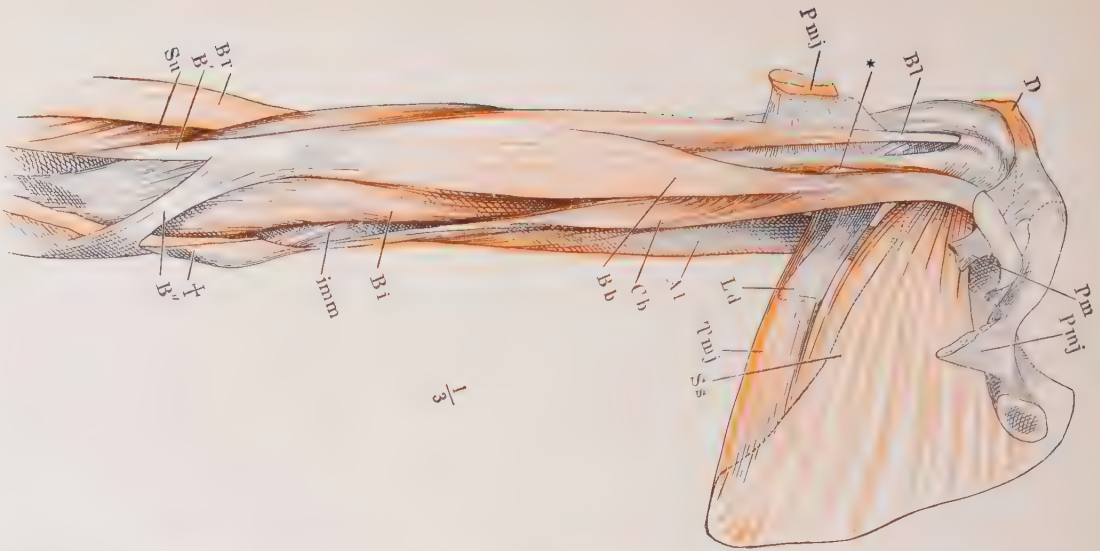


FIG. 36.—The muscles of the arm as seen from the front. *Bl*, long head, and *Bb*, short head of origin of *biceps* muscle; both heads unite in the fleshy belly which ends below in the tendon *B'*; a thin expansion, *B''*, from the latter passes to the connective-tissue membranes (*fasciæ*) around the elbow; *Cb*, *coracobrachialis* muscle; *Al*, *anconeus longus* muscle; *Bi*, *brachialis internus* muscle; *Ss*, *subscapularis* muscle; *Tmj*, *teres major* muscle; *D*, *deltoid* muscle; cut short at its origin from the acromion process of the scapula. The loose areolar tissue which invested and packed the muscles has been carefully dissected away. *Ld*, tendon of insertion of *latissimus dorsi* muscle; *Pmj*, end of collar-bone with clavicular portion of origin of *pectoralis major* muscle; *Pm*, tendon of insertion of small pectoral muscle; *, divided lateral cutaneous nerve; *Br*, brachio-radial muscle; *Su*, supinator muscle.

tendons, which being composed of inextensible white fibrous tissue transmit the movement to the hard parts to which they are attached, just as a pull at one end of a rope may be made to act upon distant objects to which the other end is tied. The tendons are merely passive cords and are sometimes very long, as for instance in the case of the muscles of the fingers, the bellies of many of which lie away in the forearm.

If the tendons at each end of a muscle were fixed to the same bone the muscle would clearly be able to produce no movement, unless by bending or breaking the bone; the probable result in such a case would be the tearing of the muscle by its own efforts. In the Body, however, the two ends of a muscle are always attached to different parts, usually two bones, between which more or less movement is permitted, and so when the muscle pulls it alters the relative positions of the parts to which its tendons are fixed. In the great majority of cases a true joint lies between the bones on which the muscle can pull, and when the latter *contracts* it produces movement at the joint. Many muscles even pass over two joints and can produce movement at either, as the biceps of the arm which, fixed at one end to the scapula and at the other to the radius, can move the bones at either the shoulder or elbow-joint. Where a muscle passes over an articulation it is nearly always reduced to a narrow tendon; otherwise the bulky bellies lying around the joints would make them extremely clumsy and limit their mobility.

Origin and Insertion of Muscles. Almost invariably that part of the skeleton to which one end of a muscle is fixed is more easily moved than the part on which it pulls by its other tendon. The less movable attachment of a muscle is called its *origin*, the more movable its *insertion*. Taking for example the *biceps* of the arm, we find that when the belly of the muscle contracts and pulls on its upper and lower tendons, it commonly moves only the forearm, bending the elbow-joint as shown in Fig. 37. The shoulder is so much more firm that it serves as a fixed point, and so that end is the origin of the muscle, and the forearm attachment, *P*, the insertion. It is clear, however, that this distinction in the mobility of the points of fixation of the muscle is only relative, for, by changing the conditions, the insertion may become the stationary and the origin the moved point; as for instance in going up a

rope "hand over hand." In that case the radial end of the muscle is fixed and the shoulder is moved through space by its contraction.

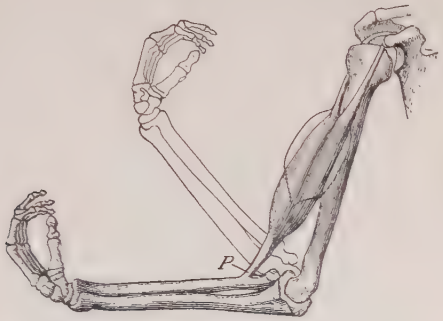


FIG. 37.—The biceps muscle and the arm-bones, to illustrate how, under ordinary circumstances, the elbow-joint is flexed when the muscle contracts.

Different Forms of Muscles. Many muscles of the Body have the simple typical form of a belly tapering to a single tendon at each end as *A*, Fig. 38, but others divide at one end and are called *two-headed* or *biceps* muscles; while some are even three-headed or *triceps muscles*. On the other hand, some muscles have no tendon at all at one end, the belly running quite up to the point of attachment; and some have no tendon at either end. In many muscles a tendon runs along one side and the fibers of the belly are attached obliquely to it; such muscles (*B*, Fig. 38) are called *penniform* or featherlike; or a tendon runs obliquely down the middle of the muscle and has the fibers of the belly fixed obliquely on each side of it (*C*, Fig. 38), forming a *bipenniform muscle*: or even two tendons may run down the belly and so form a *tripenniform muscle*. In a few cases a tendon is found in the middle of the belly as well as at each end of it; such muscles are called *digastric*. A muscle of this form (Fig. 39) is found in connection with the lower jaw. It arises by a tendon attached to the base of the skull: from there its first belly runs downwards and forwards to the neck by the side of the hyoid bone, where it ends in a tendon

FIG. 38. — Diagrams illustrating typical muscles; *a*, with a central belly and two terminal tendons; *b*, a penniform muscle; *c*, a bipenniform muscle.

which passes through a loop serving as a pulley. This is succeeded by a second belly directed upwards towards the chin, where it ends in a tendon inserted into the lower jaw. Running along the front of the abdomen from the pelvis to the chest is a long muscle on each side of the middle line called the *rectus abdominis:* it is *polygastric*, consisting of four bellies separated by short tendons. Many muscles moreover are not rounded but form wide flat masses, as for example the muscle *Ss* seen on the ventral side of the shoulder-blade in Fig. 36.

FIG. 39.—A digastric muscle.

Gross Structure of a Muscle. However the form of the skeletal muscles and the arrangement of their tendons may vary, the essential structure of all is the same. Each consists of a proper *striated muscular tissue*, which is its essential part, but which is supported by connective tissue, nourished by blood vessels, and has its activity governed by nerves so that a great variety of things go to form the complete organ.

A loose sheath of areolar connective tissue, called the *perimysium*, envelopes each muscle, and from this partitions run in and subdivide the belly into bundles or *fasciculi* which run from tendon to tendon, or for the whole length of the muscle when it has no tendons. The coarseness or firmness of butcher's meat depends upon the size of these primary fasciculi, which differs in different muscles of the same animal. These larger fasciculi are subdivided by finer connective tissue membranes into smaller ones, each of which consists of a certain number of microscopic *muscular fibers* bound together by very fine connective tissue and enveloped in a close network of blood vessels. Where a muscle tapers the fibers in the fasciculi become less numerous, and when a tendon is formed disappear altogether, leaving little but the connective tissue.

Histology of Skeletal Muscle. Each muscle-fiber is developed from a single cell and so constitutes a single histological element. In the adult form, however, a muscle-fiber differs from an ordinary cell in that it contains several nuclei. Muscle-fibers vary greatly in size; ranging in length from 1 up to 35 mm. ($\frac{1}{25}$ in. to $1\frac{1}{3}$ in.), and in diameter from 0.034 to 0.055 mm. ($\frac{1}{750}$ to $\frac{1}{450}$ in.). (See page 10.) Each fiber consists of a certain amount of muscle substance, the *muscle plasma*, inclosed in a transparent membranous sheath, the

sarcolemma. This latter structure serves not only to hold the semi-fluid muscle plasma in place, but also to transmit the pull of the contracting fiber to the point of attachment of the muscle. The most striking characteristic of a fiber's appearance is the series of alternating light and dim transverse bands of nearly equal width with which it is marked, and from which its designation as striated muscle is derived (Fig. 40). Under the high power of the

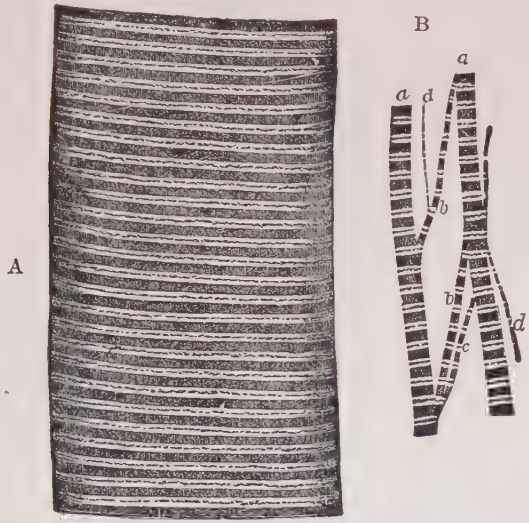


FIG. 40.—*A*, Portion of a human muscle fiber. *B*, Separated bundles of fibrils, *d*, single fibril. × 800. (Sharpey.)

microscope the muscle plasma is seen to be made up of a number of longitudinal *fibrils* of inconceivable minuteness, surrounded by a homogeneous medium, the *sarcoplasm*.

Both fibrils and sarcoplasm consist of living protoplasm; the fibrils are, however, much denser than the sarcoplasm. So far as can be judged the consistency is of minute strands of thick jelly interspersed with very thin and watery jelly. The surfaces of contact between the fibrils and the surrounding sarcoplasm are looked upon as the actual seats of energy liberation; in other words, the utilization of surface energy in muscle depends on changes brought to bear at the fibrillar surfaces (p. 112). The cross striations, that are much more conspicuous under the microscope than the outlines of the longitudinal fibrils, consist of alternating

light and dim transverse bands; they are thought to be due to differences of consistency, or possibly of actual chemical composition, that recur at regular intervals along the length of each fibril. Fine dark lines at the middle of each light area apparently indicate the presence of delicate transverse membranes by which the fibrils are subdivided into segments (B, Fig. 40). How the cross striations are related to the liberation of energy; in other words, what part they play in the working of the muscle machinery, is not known.

Since the fiber as a whole contains many fibrils and since the cross striations are regular throughout the entire fiber it follows that all the fibrils of any fiber must have their segments at corresponding levels. The fibrils are probably kept in place by an interfibrillar network of some sort.

The blood vessels and nerve-fibers supplied to the skeletal muscles are numerous. The larger blood vessels run in the coarser partitions of the connective tissue lying between the fasciculi and

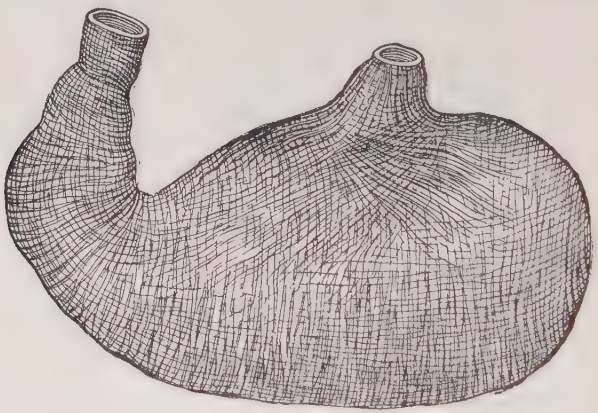


FIG. 41.—The muscular coat of the stomach.

give off fine branches which form a network between the individual fibers but never penetrate the sarcolemma.

Connected with each muscle-fiber are one or more nerve-fibers. The central core of each nerve-fiber ends in an oval expansion (*end plate*) which contains many nuclei and lies close under the sarcolemma, its deeper side being in immediate contact and possibly continuous with the striated contents. These nerve-fibers are *motor* or concerned in exciting a contraction of the muscle-fiber.

Other nerve-fibers are connected with very peculiar bodies found scattered throughout the muscle, but especially numerous near the tendons. They are usually of a size just visible to the unaided eye and from their form have been named *muscle-spindles*. They are sensory in function. Somewhat similar bodies (Golgi's *tendon-organs*) are found in the tendons and are also richly supplied with nerve-fibers.

Structure of the Smooth Muscles. Of these the muscular coat of the stomach (Fig. 41) is a good example. They have no definite tendons, but form expanded membranes surrounding cavities, so that they have no definite origin or insertion. Like the skeletal muscles they consist of proper contractile elements, with accessory connective tissue, blood vessels, and nerves. Their fibers, however, have a very different microscopic structure. They present a slightly marked longitudinal but no cross striation and are made up of elongated cells (Fig. 42), bound together by a small quantity of cementing material. The cells vary considerably in size, but on the average are about $\frac{1}{24}$ mm. ($\frac{1}{600}$ in.) in length. Each is flattened in one plane, tapers off at each end, and possesses a very thin enveloping membrane; in its interior lies an elongated nucleus. These cells have the power of shortening in the direction of their long axes, and so of diminishing the capacity of the cavities in the walls of which they lie.

FIG. 42.—Isolated smooth muscle cells from human small intestine.

Cardiac Muscular Tissue. This consists of nucleated branched cells which unite to form a network, in the interstices of which blood-capillaries and nerve-fibers run. The cells present transverse striations, but not so distinct as those of the skeletal muscles, and are said to have no sarcolemma (Fig. 43).

Ciliated Cells. As the growing Body develops from its primitive simplicity we find that the cells lining some of the tubes and cavities in its interior undergo a very remarkable change, by which each cell differentiates itself into a nutritive and a highly motile portion. Such cells are found for example lining the wind-

pipe, and are represented in Fig. 44. Each has a conical form, the base of the cone being turned to the cavity of the air-tube, and contains an oval nucleus. On the broader free end are a number (about thirty on the average) of extremely fine processes called *cilia*. During life these are in constant rapid movement, lashing to and fro in the liquid which moistens the interior of the passage; and as the cells are very closely packed, a bit of the inner surface of the windpipe, examined with a microscope, looks like a field of wheat or barley when the wind blows over it. Each cilium strikes with more force in one direction than in the opposite, and as this direction of more powerful stroke is the same for all the cilia on any one surface, the resultant effect is that the liquid in which they move is driven one way. In the case of the windpipe for example it is driven up towards the throat, and the tenacious liquid or mucus which is thus swept along is finally coughed or "hawked" up and got rid of, instead of accumulating in the deeper air-passages away down in the chest.

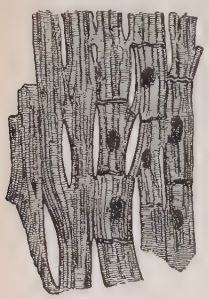


Fig. 43.—Cardiac muscular tissue, magnified about 400 diameters. The cell-boundaries and cell-nuclei are indicated only in the right-hand portion of the figure.

These cells afford an extremely interesting example of the division of physiological employments. Each proceeds from a cell which was primitively equally motile and nutritive in all its parts. But in the fully developed state the nutritive duties have been especially assumed by the conical cell-body, while the contractile properties have been condensed, so to speak, in that modified portion of the primitive protoplasmic mass which forms the cilia. These, being supplied with elaborated food by the rest of the cell, are raised above the vulgar cares of life and have the opportunity to devote their whole attention to the performance of automatic movements; which are accordingly far more rapid and precise than those executed by the whole cell before any division of labor had occurred in it.

Fig. 44.—Ciliated cells.

That the movements depend upon the structure and composition of the cells themselves, and not upon influences reaching them

from the nervous or other tissues, is proved by the fact that they continue for a long time in isolated cells, removed and placed in a liquid, as blood-serum, which does not after their physical constitution. In cold-blooded animals, as turtles, whose constituent tissues frequently retain their individual vitality long after that bond of union has been destroyed which constitutes the life of the whole animal as distinct from the lives of its different tissues, the ciliated cells in the windpipe have been found still at work three weeks after the general death of the animal.

The Chemistry of Muscular Tissue. When we subject a mass of muscle to chemical analysis we, of course, kill the fibers, if they were not dead when the analysis was started. The difference between life and death is undoubtedly at bottom a chemical or physico-chemical difference, so that we cannot hope by the ordinary methods of analysis as applied to dead tissues to learn the exact chemistry of the living muscles. On the other hand, the constituents we find in dead muscle were derived from those of the living muscle, and are undoubtedly nearly related to them, so that knowledge of the chemistry of dead muscle cannot fail to give us a degree of insight into the nature of the living muscle.

To understand clearly the facts brought out by an analysis of muscle we need to bear in mind that a muscle, as stated previously, is an engine, whose property is to convert chemical energy into mechanical. Our analysis will demonstrate the presence of some substances which are part of the machinery; of others which make up the fuel from which the energy for operation is derived; of still others which are nothing more than the waste products from previous activity. It is as though a locomotive in full career suddenly fell into so deep a chasm as to reduce it with its tender to a mass of indistinguishable fragments. Chemical examination of the mass would bring to light various materials, such as steel, brass, and nickel, which were part of the engine; coal, which was the fuel; and ashes, representing the waste products. In similar fashion we may pick out from a chemical study of muscle some constituents which probably represent the machinery; others which form the fuel; and still others which are waste substances.

The most abundant single constituent of muscle is water, which forms 75 per cent of its mass. Dissolved in the water are small quantities of a number of simple inorganic salts, chiefly chlorides

and carbonates of potassium, sodium, and magnesium. Since experiment has shown that these salts, as well as the water in which they are dissolved, are essential to the life and operation of the muscle we may look upon them as part of the machinery. Similarly, the most abundant solid constituents of muscle, the proteins, are to be included as portions of the mechanism.

At least three proteins have been obtained from mammalian striated muscle, *myogen*, and *myosin*, both coagulable by heat, and a protein which is insoluble in pure water or dilute saline solution and which appears to form a framework within the fiber. This latter is called the *muscle stroma* and constitutes 9 per cent of the weight of striated muscle. Muscle tissue contains three or four times as much myogen as myosin. Both of these proteins possess the property of passing over into insoluble forms known respectively as myogen fibrin and myosin fibrin.

Heart muscle contains relatively much less myogen and myosin and much more stroma than does ordinary striated muscle, its stroma constituting 56 per cent of its weight. Smooth muscle contains an even larger proportion of stroma, 72 per cent. In striated muscle the proteins appear to be confined largely to the fibrils, except in so far as the sarcolemma is protein in constitution.

Another constituent of muscle which is apparently part of the contractile machinery is the relatively simple nitrogenous compound *creatine* (p. 22). Recent studies of the part played by this substance in tissue indicate that living protoplasm always contains it, and suggest that it may be an essential part of the chemical complex upon which life depends.

The known fuel substances found in muscle are two, *glucose*, which is found in very small amount, and *glycogen*, which forms about 1 per cent of the weight of the muscle. The muscle is probably able to use other substances as fuel, fats, for example, but chemical analysis does not enable us to distinguish these from similar substances which belong to the mechanism.

Urea and other nitrogenous extractives are found in muscle also. These are to be classed as waste products, but an interesting and important fact is that they are formed just as rapidly in a resting muscle as in one that is active; in other words, they are products of basic metabolism, not of functional (p. 24). Another interesting and very significant fact is that a muscle analyzed imme-

diately after a period of vigorous activity is found to contain *lactic acid*, or the compound of this acid with sodium, sodium lactate, whereas muscles that have been resting do not contain lactates. This fact, as we shall see, has important bearing on the question of the nature of muscle contraction. We shall recur to it in connection with the analysis of the process of contraction. *Carbon dioxid*, or rather its product formed in the presence of water, *carbonic acid*, is given off continuously by muscles, but more rapidly when at work than when at rest. This product indicates the presence of oxidations.

Beef Tea. From the facts about muscle proteins, stated above, it is clear that when a muscle is boiled in water its myogen and myosin are coagulated and left behind in the meat. Beef tea as ordinarily made, then, contains little but the flavoring matters and salts of the meat and some gelatin, the latter derived from the connective tissues of the muscle. The flavoring matters and salts make it deceptively taste as if it were a strong solution of the whole meat, and the gelatin causes it to "set" on cooling, so the cook feels quite sure she has got out "all the strength of the meat," whereas the beef tea so prepared contains but little of the most nutritious protein portions, which in an insipid shrunken form are left when the liquid is strained off. Various proposals have been made with the object of avoiding this and getting a really nutritive beef tea; as for example chopping the raw meat fine and soaking it in strong brine for some hours to dissolve out the myogen; or extracting it with dilute acids which dissolves the myogen and myosin and at the same time render it noncoagulable by heat when subsequently boiled. Such methods, however, make unpalatable compounds which invalids will not take. Beef tea is a slight stimulant, and often extremely useful in preparing the stomach for other food, but its direct value as a food is slight, and it cannot be relied upon to keep up a patient's strength for any length of time. There can be no doubt that thousands of sick persons have in the past been starved to death on it. Commercial *meat extract* is essentially a very strong beef tea; containing much of the flavoring substances of the meat, nearly all its salts and the crystalline nitrogenous bodies, such as creatine, which exist in muscle, but hardly any of its really nutritive parts. From its stimulating effects it is often useful to persons in feeble health, but

other food should be given with it. It may also be used on account of its flavor to add to the "stock" of soup and for similar purposes; but the erroneousness of the common belief that it is a highly nutritious food cannot be too strongly insisted upon.

Rigor Mortis. During life and for a certain time after general death the muscles are soft, translucent, extensible and elastic, and neutral or feebly alkaline in reaction; after a period which in warm-blooded animals is brief (varying from a few minutes to three or four hours) they gradually become harder, more opaque, less extensible and less elastic, and distinctly acid in reaction. The result of these changes is the well-known cadaveric rigidity or *rigor mortis*. It was formerly very generally believed that the cause of rigor is the change of soluble myogen and the myosin to insoluble myogen fibrin and myosin fibrin. Quite recently, however, it has been shown that death stiffening is primarily due to the considerable production of lactic acid which accompanies the death process. In line with this fact is the well-known tendency of animals or men killed suddenly in the midst of violent exertion to stiffen very quickly. Men killed in battle often retain the postures in which death overtook them. Hard muscular work involves a large production of lactic acid, a condition favorable to a prompt onset of rigor.

CHAPTER VII

MUSCULAR ACTIVITY

The Study of Isolated Muscles. There are some simple facts of muscle activity that one can learn by observing his own muscles; for example, when the arm is bent at the elbow the muscle that produces the movement, the biceps, can be seen under the skin to shorten and thicken, and if felt will be found hard when contracted, as compared with its soft flabbiness when relaxed. This knowledge is the possession of every schoolboy.

More detailed knowledge can be gained by the direct examination of living muscles, dissected away from their bodily attachments. To isolate the muscles of the higher animals thus is obviously impractical, but fortunately the "cold-blooded" animals, notably frogs and turtles, are peculiarly suited for such studies as this. If a frog is quickly killed, as by destroying the brain with a sharp instrument, the large muscle of the calf of the leg, the *gastrocnemius*, can be dissected out, and if properly cared for will remain alive for several hours, during which its activity can be studied. The chief precaution to be observed is to prevent such evaporation of water from the muscle as would disturb the physico-chemical equilibrium and injure the tissue. This loss of water is prevented by repeated moistening, but here again a precaution must be observed since the application of pure water to the surface of the muscle would be followed by a flow of water into the tissue under the driving force of *osmotic pressure* (p. 32). This would bring about a disturbance of equilibrium in the direction of too great dilution as harmful to the tissue as the evaporation it is designed to prevent. For moistening the muscle a liquid of the same osmotic pressure as the tissue fluids must be employed. A solution of common salt with a concentration of 0.7 per cent satisfies this condition and is the fluid commonly used for keeping living tissues moist.

The Necessity of Stimulation. An important fact about skeletal muscle, one indeed which has much to do with the adaptive character of its action, is that it remains in a condition of inac-

tivity except when in receipt of definite stimulation. A moment's thought will show the importance of this property. The usefulness of a muscle depends quite as much upon its ability to be inactive when not wanted as upon its property of contracting when contraction is desired. The difficulties frequently experienced by sufferers from *chorea* (St. Vitus Dance) illustrate this point sufficiently.

For the study of activity in isolated muscles some form of artificial stimulation must be employed. By far the most satisfactory is an electric shock such as may be generated by a small induction coil. By carrying fine wires from the terminals of the coil to opposite ends of the muscle the latter becomes a part of the circuit. Thus when the coil discharges a spark the muscle receives it and is stimulated. Besides being peculiarly effective as stimuli induction shocks have the advantage of being easily modified in intensity, and, when not excessive, of having no injurious effect on the tissue.

A Simple Muscular Contraction. When a single electric shock is sent through a muscle, it rapidly shortens and then rapidly lengthens again. The whole series of phenomena from the moment of stimulation until the muscle regains its resting form is known as a *simple muscular contraction* or a *"twitch"*: it occupies in frog's muscle about one-tenth of a second. So brief a movement as this cannot be followed in its details by direct observation, but it is possible to record it and study its phases at leisure. This may be done by firmly fixing the upper tendon of an isolated muscle, *M*, Fig. 45, and attaching the other end at *d* to a lever, *l*, which can move about the fulcrum *f*: the end of the long arm of the lever bears a point, *p*, which scratches on a smooth smoked surface, *S*. Suppose the surface to be placed so that the writing point of the lever is at *a*; if the muscle now contracts it will raise the point of the lever, and a line *ac* will be drawn on the smoked surface, its vertical height, *cm*, being dependent, first, on the extent of the shortening of the muscle, and second, on the proportion between the long and short arms of the lever: the longer *fp* is as compared with *fd*, the more will the actual shortening of the muscle be magnified. With the lever shown in the figure this magnification would be about ten times, so that one-tenth of *cm* would be the extent of the shortening of the muscle. Suppose, next, the

smoked surface to be moved to such position that the writing point of the lever touches it at *i*, and, the muscle being left at rest the surface to be moved evenly from left to right; the horizontal line *io* would then be traced, its length depending on the distance through which *S* moved during the time the lever was marking on it: and it is clear that if *S* move uniformly, and we know its rate of movement, we can very readily calculate from the length of *io* how long *S* was moving while that line was being traced: for example, if we know the rate of movement to be ten centimeters per second, and on measurement find *io* to be one centimeter long, the

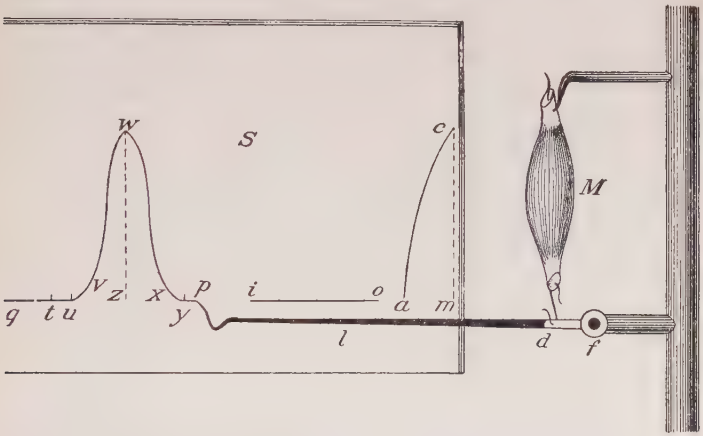


FIG. 45.—Diagram to illustrate the method of obtaining a graphic record of a muscular contraction.

time during which the surface was moving must have been 0.1 second; and each tenth of *io* correspond to 0.01 second.

If we set the recording surface in motion and while the lever point is tracing a horizontal line cause the muscle to contract, the point will be raised as long as the muscle is contracted, and the line drawn by it will be due to a combination of two simultaneous movements—a horizontal, due to the motion of *S*, and a nearly vertical, due to the shortening of the muscle; the resulting line is a curve known as *the curve of a simple muscular contraction*. Let the surface *S* be placed so that the writing point is at *q* and then be set in uniform motion from right to left at the same rate as before (ten centimeters per second). When the point is opposite *t*, stimu-

late the muscle by an electric shock; the result, until the muscle has fully lengthened again, will be the curve *tuwxy*, from which many things may be learned. In the first place we see that the muscle does not commence to contract at the very instant of stimulation, but at an appreciably later time, and during the interval the lever draws the horizontal line *tu;* this period, occupied by preparatory changes within the muscle, is known as *the latent period*. Then the muscle begins to shorten and the lever to rise, until the summit of the contraction is reached at *w*. The muscle then, but only gradually passes back to the resting state, tracing the line *wxy*. The curve shows three distinct phases in the contraction: the latent period; the period of shortening; the period of relaxation. Knowing the rate of horizontal movement, we can measure off the time occupied by each phase. The horizontal distance from *t* to *u* represents the time taken by the latent period; from *u* to *z*, the time occupied in shortening; from *z* to *y*, the time taken in elongation; in a fresh frog's muscle these times are respectively 0.01, 0.04, 0.05 second. In the muscles of warm-blooded animals they are all shorter, but the difficulties in the way of accurate experiment are very great. If we know the relative lengths of the arms of the lever we can of course readily calculate from the height, *wz*, of the curve the extent of shortening of the muscle. With a single electrical stimulation this is never more than one-fourth the total length of the muscle.

In Fig. 45 the accessory apparatus used in practice to indicate on the moving surface the exact instant of stimulation and to measure the rate at which *S* moves have been omitted.

The Influence on Contraction Height of Increasing Stimulation Strength. If an isolated muscle is stimulated at regular intervals, as once in two seconds, by induction shocks made stronger each time, there will be at first, if the shocks to begin with are weak enough, no visible response. Presently, as stronger shocks are used, barely perceptible twitches are given. These become higher and higher as the stimuli are increased until a point is reached beyond which no further increase in height appears, no matter how much the intensity of the shock may be increased. These highest contractions which the muscle is capable of giving as the result of any single stimulus, however strong, are called *maximal* contractions.

Every skeletal muscle, even the smallest, is made up of a great number of fibers. This must be borne in mind when we attempt to explain the production of graded responses, for when the muscle contracts feebly it may be that all the fibers are contracting, each one feebly, or it may be that a few fibers scattered through the muscle are contracting powerfully while the others are inactive. The former view was generally held until recently, when careful direct experimentation demonstrated that individual fibers contract to their full power under the conditions prevailing at the instant of stimulation, or else do not contract at all. This principle of action, known as the "all or nothing" principle, we now know to be of widespread application in Physiology. Not only do muscle fibers contract in accordance with it, but nerve fibers transmit impulses of full size or not at all, thus obeying the same law. It should be said that the "all or nothing" principle of action follows almost of necessity from the fact that functional activity is based on chemical and physico-chemical processes: for a fundamental principle of chemistry is that reactions once started go on without interruption until an equilibrium is attained. If one sets fire to a heap of gunpowder he expects it to go on burning until either the powder or the available oxygen is used up: similarly, if one excites a muscle fiber to contract he may expect the processes started within it to run on to completion. Since the fiber has the power of making a strong contraction the making of a feeble contraction would involve a stoppage of the contractile process in full career, something we cannot reconcile with our conception of the chemical nature of muscular activity. We constantly produce graded movements in our own Bodies. According to the view just expressed the grading is obtained by varying the number of fibers called into play. Since each muscle fiber has a nerve fiber connecting with it, this implies the throwing of more or fewer nerve fibers into action, as powerful or feeble contractions are evoked.

The Influence of Temperature on Contraction. If an isolated muscle is cooled down and then stimulated, the contraction will occur much more slowly than at ordinary temperatures. On the other hand a muscle that is warmed contracts and relaxes more rapidly than one that is at room temperature. This variation in the speed of contraction with change of temperature is in accord

with a general chemical law which states that chemical processes are more rapid at higher temperatures than at lower; a law which applies to muscular contraction because the mechanical act of shortening is based on a preceding chemical process. In nature the influence of temperature on muscular contraction is seen only in the lower (cold-blooded) animals, whose bodies are at substantially the temperature of the surroundings and which, as can easily be observed, are sluggish in cold weather and active in warm. In man and the higher (warm-blooded) animals, and in birds, which are also warm-blooded, the body temperature is high and relatively constant, and the muscles are not subjected, therefore, to such temperature variations as occur in lower forms. One advantage of the warm-blooded state is that it insures for the muscles a favorable temperature for effective operation in cold weather as well as in warm.

Heat Rigor. If an isolated muscle is heated above 40–45° C. (104–113° F.) it is killed by the heat and undergoes a marked contraction known as *heat rigor*. Heat rigor like the death stiffening (rigor mortis, p. 100) is accompanied by, and probably caused by, a great production of lactic acid within the muscle.

The Measure of Muscular Work. The work done by a muscle in a given contraction, when it lifts a weight vertically against gravity, is measured by the weight moved, multiplied by the distance through which it is moved. When a muscle contracts carrying no load it does very little work, lifting only its own weight; when loaded with one gram and lifting it five millimeters it does five gram-millimeters of work, just as an engineer would say an engine had done so many kilogrammeters or foot-pounds. If loaded with ten grams and lifting it six millimeters it would do sixty gram-millimeters of work. Even after the weight becomes so great that it is lifted through a less distance, the work done by the muscle goes on increasing, for the heavier weight lifted more than compensates for the less distance through which it is raised. For example, if the above muscle were loaded with fifty grams it would maybe lift that weight only 1.5 millimeters, but it would then do 75 gram-millimeters of work, which is more than when it lifted ten grams six millimeters. A load is, however, at last reached with which the muscle does less work, the lift becoming very little indeed, until at last the weight becomes so great that the muscle

cannot lift it at all and so does no work when stimulated. Starting then from the time when the muscle carried no load and did no work, we pass with increasing weights, through phases in which it does more and more work, until with one particular load it does the greatest amount possible to it with that stimulus: after that, with increasing loads less work is done, until finally a load is reached with which the muscle again does no work. What is true of one muscle is of course true of all, and what is true of work done against gravity is true of all muscular work, so that there is one precise load with which a beast of burden or a man can do the greatest possible amount of work in a day. With a lighter or heavier load the distance through which it can be moved will be more or less, but the actual work done always less. In the living Body, however, the working of the muscles depends so much on other things, as the due action of the circulatory and respiratory systems and the nervous energy or "grit" (upon which the stimulation of the muscles depends) of the individual man or beast, that the greatest amount of work obtainable is not a simple mechanical problem as it is with the excised muscle.

Influence of the Form of the Muscle on its Working Power. The amount of work that any muscle can do depends of course largely upon its physiological state; a healthy well-nourished muscle can do more than a diseased or starved one; but allowing for such variations the work which can be done by a muscle varies with its form. The thicker the muscle, that is, the greater the number of fibers present in a section made across the long axes of the fasciculi, the greater the load that can be lifted or the other resistance that can be overcome. On the other hand, the extent through which a muscle can move a weight increases with the length of its fasciculi. A muscle a foot in length can contract more than a muscle six inches long, and so would move a bone through a greater distance, provided the resistance were not too great for its strength. But if the shorter muscle had double the thickness, then it could lift twice the weight that the longer muscle could. We find in the Body muscles constructed on both plans; some to have a great range of movement, others to overcome great resistance, besides numerous intermediate forms which cannot be called either long and slender or short and thick; many short muscles for example are not specially thick, but are short

merely because the parts on which they act lie near together. It must be borne in mind, too, that many apparently long muscles are really short stout ones—those namely in which a tendon runs down the side or middle of the muscle, and has the fibers inserted obliquely into it. The muscle (*gastrocnemius*) in the calf of the leg, for instance (Fig. 38, *C*), is really a short stout muscle, for its working length depends on the length of its fasciculi and these are short and oblique, while its true cross-section is that at right angles to the fasciculi and is considerable. The force with which a muscle can shorten is very great. A frog's muscle of 1 square centimeter (0.39 inch) in section can just lift 2,800 grams (98.5 ounces), and a human muscle of the same area more than twice as much.

The Source of Muscular Energy. In the physical sense a muscle is a machine. By this we mean that whatever energy it gives out must have been supplied to it previously from the outside. The work which a muscle does in contracting is at the expense of its available store of energy. We know that the energy exhibited by a steam-engine is derived from the combustion or oxidation of the fuel under the boiler. We know also that the energy exhibited by a contracting muscle is derived from the oxidation of fuel substances within it. The physical accompaniments of oxidation are not the same in the two cases; the fuel under the boiler burns with flame and at a high temperature; the fuel substance within the muscle burns without flame and at a temperature only slightly higher than that of the body. The energy yield, however, for corresponding amounts of fuel is as great in one case as in the other.

The fuel substances used in the Body are chiefly glucose or the closely related substance glycogen, and fats. That the third group of energy yielding foods, the proteins, are not ordinarily used as fuel for the muscles was proven by a very interesting experiment which stands as one of the classical experiments in Physiology. The proof rests upon the fact that the decomposition of proteins gives rise to compounds which contain nitrogen and which are discharged from the Body, except for a negligible residue, by way of the kidneys. If the urine is collected and its nitrogen content determined, the amount of protein decomposition that has occurred in the Body can be calculated (see table, p. 21).

Two German Physiologists, Fick and Wislicenus, determined their average daily loss of nitrogen over a period of several days of relative inactivity and then engaged in a day of exceptionally vigorous muscular exercise. The form of activity chosen was mountain climbing; the mountain ascended was the Faulhorn in the Alps, 1,956 meters (6,000 feet) high. In spite of the very great increase in the amount of muscular energy manifested, and the consequent great increase in the amount of fuel consumed, the total loss of nitrogen from the Body was virtually the same as on the previous and subsequent days of inactivity. This experiment, which has been repeated and confirmed many times, shows that proteins are not ordinarily used by the muscles as fuel. Therefore the other energy-yielding foods must serve. (See also Chap. XXX.)

While fats are excellent fuel foods, and are, in all likelihood, used by the muscles when brought to them by the blood, there is abundant evidence that the muscles can get along without fats provided they have enough fuel in the form of sugar. When sugar or fats are burned the products of the oxidation are carbon dioxid and water. The reaction in the case of sugar is represented by the equation $C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O$. That one or the other of the fuel substances mentioned above is oxidized during muscular activity is shown by an increase in the amount of carbon dioxid produced in the Body and breathed out from the lungs. By a comparatively simple device the amount of carbon dioxid breathed out per minute can be determined, and there is invariably a pronounced increase during and immediately following muscular exercise. If the exercise is sharp the increase may be 8–10 fold. There is, of course, an equivalent increase in water production, but the water so produced merely adds itself to the abundant water already present in the Body and cannot be identified as can the gaseous carbon dioxid.

The Energy Relationships of Contracting Muscle. Muscular Efficiency. Since the muscle is an engine for the conversion of one kind of energy (chemical) into another kind (mechanical) its energy relationships can be studied in the same manner as in other sorts of engines. We are familiar with various classes of these. A steam power plant and an automobile fall in the same group with muscles in that they are devices for transforming chemical energy

(oxidation of fuel) into mechanical. A hydro-electric installation converts the mechanical energy of the waterfall into electrical energy. An ordinary dry cell is an engine for the conversion of chemical energy into electrical, and a motor for the conversion of electrical energy into mechanical. All these engines have in common the feature of relative inefficiency. When we speak of the efficiency of an engine we mean the ratio of the amount of useful energy it gives out to the total amount it uses up. No engine is 100 per cent efficient; in none can all the energy put in be recovered in available form. There is always a fraction of the total energy which manifests itself in the form of heat. The hot flue gases from the furnace and the hot water in the cooling system of the automobile signify energy which, from the standpoint of the machine, is wasted. Muscles share with other engines this feature of inefficiency. As used in the Body the muscles are only about 20 per cent efficient. That is, in order to do a given amount of muscular work we must burn in our bodies enough fuel to give a total energy output five times as great. The balance, of 80 per cent, takes the form of heat, and explains why we find ourselves so warm after vigorous exercise.

Energy Units. In order to be able to discuss energy relationships intelligently we need to have some means of designating definite amounts. The form of energy into which all other forms tend to convert themselves is, as we have seen, heat. A convenient energy unit, then, is the heat unit. The amount of heat required to raise the temperature of 1 gram ($\frac{1}{28}$ oz.) of water 1 degree centigrade (strictly from 14° to 15°) is taken as the unit. This is known as the *calorie*. For convenience when large amounts of heat are involved a second unit just one thousand times as great is also used. This is called the *kilocalorie* or simply the *large Calorie*, distinguished from the small calorie by the use of the capital initial. Although the calorie is strictly a heat unit it serves as an expression for any form of energy. If we speak of any engine as able to furnish a certain number of calories we mean that *if all the energy were to appear as heat* that many calories would be liberated. As a matter of fact much of the energy may actually take other forms, as it does in the case of the contracting muscle.

When the energy is manifested as mechanical work it is measured in terms of the work done. Since the simplest form of work

is probably the raising of weights against the resistance of gravity the units of work are based on weight and height. Thus the *foot-pound* is the amount of energy involved in raising a weight of one pound to a height of one foot. A calorie is approximately equivalent to 3 foot-pounds. In the metric system the unit of mechanical energy is the *gram-centimeter*. In round numbers 41,000 gram-centimeters represent the same amount of energy as 1 calorie.

The Energy Output of Muscle. Studies of the mechanical energy developed by selected groups of muscles in the Body can be made directly. An excellent method is by means of a stationary bicycle. The wheel can be made to revolve against a measured resistance, and thus the work done can be readily determined. As already stated, muscles in the Body work very inefficiently. This is mainly due to the mechanical disadvantages at which muscles work. They pull at the short arms of levers, and the direction of their pull is usually oblique (Chap. VIII). The energy output of an isolated muscle is also easy to determine, although to be certain that the utmost possible has been obtained is not so simple. The muscle operates by forcible shortening. That means that the muscle pulls upon the weight to which it is attached. If the tension developed is greater than the weight the latter is lifted and work is done. If the tension is insufficient to raise the weight there is no manifestation of mechanical energy. All the energy liberated takes the form of heat. It has been found that in a given muscle under given conditions the *tension developed* is fairly constant and directly proportional to the total energy manifested in the contraction; whereas the actual mechanical work done depends, as we have already seen (p. 106) on various factors, such as the relation of the load to the absolute strength of the muscle.

In the study of the muscle as an engine knowledge of the energy relationships is of the greatest moment. We know that muscular activity is based on chemical transformations, and to explain the actions of the muscle we must know what these chemical transformations are. If we assume any particular transformation to be the one from which the muscle derives its energy we must be able to show that that transformation yields the amount of energy which the muscle actually manifests. If it does not do so the assumption which selected it as the source of the muscle's power is obviously erroneous.

The Immediate Energy of Muscular Contraction. While the muscle is, as stated above, an engine which in the long run operates on the basis of energy derived from the burning of fuel there is abundant evidence that the actual act of contraction is not brought about by that means. The energy present in the form of surface energy (p. 28) is released in such a way as to cause the muscle fibers to develop tension; in developing this tension the store of energy is depleted; the oxidation process then occurs and the energy store is renewed. A very good analogy is suggested by the ordinary steam-driven pile driver. The weight falls when released, and in falling does mechanical work and produces heat; before further work can be done some fuel must be burned under the boiler, and the energy thus obtained utilized to draw the weight back up again.

Proof that the oxidation *follows* contraction rather than *precedes* it has been gained in various ways; by an extremely delicate registering device the surplus heat that always attends oxidation processes has been measured, and found to be given out, in the simple twitch, after the contraction itself is nearly or entirely over. Furthermore, freshly isolated muscles can be placed in a vacuum, or more simply in an atmosphere consisting wholly of nitrogen, and will respond for several twitches precisely as well as in air. It has been proved, incidentally, that muscles have no store of oxygen within themselves on which they draw under these circumstances; nor do they give off carbon dioxid when contracting in an atmosphere devoid of oxygen. These contractions are performed without any aid whatever from oxidation. We are obliged to conclude that the release of surface energy does not result from an oxidation, but from some other form of chemical or physico-chemical change.

Lactic Acid Production the Salient Feature. In the last chapter the fact was mentioned that active muscles produce lactic acid in connection with their contraction. It has been pretty conclusively demonstrated in recent years that this acid is formed during the contraction process itself, and the accepted theories of muscular contraction make the production of acid the means by which the release of energy is brought to pass. The present view is that a sudden increase in acidity at the surfaces of the fibrils is what causes the latter to develop tension. Lactic acid

functions by virtue of being an acid, and not through any special properties it may have that other acids do not share. We must admit that present knowledge does not go so far as to suggest why the fibrils should exert tension when their surfaces are acidified, but future study will probably show why this is so. In the meantime our analysis of muscular action can go no farther than to deal with the production of lactic acid, how it is disposed of when the contraction is over, how the energy requirements are satisfied, and what the relation of the burning of fuel is to the whole process.

The Precursor of Lactic Acid. If stimulating a muscle causes lactic acid to be suddenly produced in its fibers there must be some precursor from which the acid is obtained. The obvious precursor is glucose or a derivative, for glucose contains exactly the same elements as lactic acid in exactly the same proportion, although in twice the amount per molecule. The relationship is expressed by the equation $C_6H_{12}O_6 \rightleftharpoons 2C_3H_6O_3$, the latter symbol being that of lactic acid. The arrangement of atoms in the molecule is not the same, although not so different but that the conversion of either compound into the other can be readily effected. Two difficulties have presented themselves in the way of accepting glucose itself as the lactic acid precursor. The first is that glucose is a very stable chemical compound, while the acid precursor would be expected to be unstable, since the acid is produced with explosive suddenness. To meet this difficulty the suggestion has been offered, supported by chemical evidence obtained from the study of muscle tissue, that the glucose becomes bound up with phosphoric acid in a highly unstable compound, which breaks down when the muscle is stimulated, in such a way as to set lactic acid free. The second difficulty, which for a time seemed insuperable, arises from the energy conditions that must be satisfied. We know that in a maximal twitch about 1.3 calories of energy are set free for each gram of muscle contracting. We know also that about 0.004 gram of lactic acid is produced per gram of muscle in making the same twitch. It follows that the process by which 0.004 gram of lactic acid is produced must set 1.3 calories of energy free. Glucose has a slightly higher energy-value than lactic acid, so that when the former is converted into the latter energy is released. When the conversion was made in the laboratory, however, the amount of energy set free fell considerably short of

the figure given above; nor did the combination of glucose with phosphoric acid promise a compound enough above the energy-level of lactic acid to meet the requirement. Fortunately the use of more precise experimental methods, and of materials of utmost purity, has recently given energy figures that almost exactly correspond with the values needed, so that we are now able to state that glucose, or an unstable glucose compound, is in all probability the precursor of lactic acid in muscular contraction.

The Act of Relaxation. A muscle that is caused to give a simple twitch, by means of a single stimulus, contracts rapidly and then immediately relaxes. If we are correct in thinking that the contraction is due to acidification of the fibrillar surfaces then relaxation must be due to removal of the acid and restoration of the same surfaces to their former state. In a fresh muscle relaxation is practically as rapid as contraction, while in a muscle that has been stimulated repeatedly relaxation may be several times slower (p. 119). These differences in relaxation rate show that the act is not a simple falling back of structures that have been drawn out of position, but is a definite process, based on changes taking place in the muscle. It is fairly clear that the primary change is the union of lactic acid with sodium compounds, of which muscle has ample store, to form *sodium lactate*. The latter is a neutral salt, and by its formation the acidity of the fibrillar surfaces is done away with; the force holding the fiber in tension thus disappears, and relaxation necessarily ensues.

Muscular Activity in the Absence of Oxygen. The statement has already been made that muscles can function for a time in an environment devoid of oxygen, and without performing any oxidations, as indicated by non-evolution of carbon dioxid. By piecing together various facts that have been set forth in earlier paragraphs we may now be able to form a picture of how this is possible. The muscle has in it to start with a small quantity of glucose and a relatively large quantity of glycogen (p. 98) available as possible sources of the phosphoric acid compound which is assumed to be the actual precursor of lactic acid. Since muscles are able to contract whenever stimulated, without any special previous preparation, we have to assume that a certain amount of the precursor is formed spontaneously and held in the muscle fibers. The amount is presumably not great; although

the compound is so unstable that an actual measurement would probably be impossible. From the known laws of chemistry an equilibrium between glucose, glycogen, and "glucose-phosphate," in which small quantities of the first and third are regularly associated with large quantities of the second, can readily be pictured.

The effect of a stimulus is to upset the equilibrium obtaining in the resting fiber in such a way that the "glucose phosphate" starts to decompose into simpler compounds, of which lactic acid is the important one. This process once started must continue either until all the "glucose phosphate" is used up or until brought to an end by some other means. In fact it appears that the reaction is "self-limited" in that as the acidity rises, due to the formation of lactic acid, the decomposition of "glucose phosphate" slows down; and when a certain degree of acidity is attained stops altogether. Thus the process set off by the stimulus comes to an end while there is still a supply of acid precursor present. Meanwhile the acidification of the fibrillar surfaces has resulted in development of tension, and so in contraction. The acid immediately reacts with sodium bicarbonate, forming sodium lactate and carbonic acid; the latter is too weak an acid to be effective in maintaining tension, hence the muscle promptly relaxes.

The net chemical result of the stimulation has been to deplete the muscle of some of its "glucose phosphate" and sodium bicarbonate and to increase its concentration of sodium lactate and carbonic acid. The latter decomposes into water and carbon dioxid, and the dioxid escapes into the surrounding space, whether a vacuum or an atmosphere of nitrogen; thus the increase in lactate is the only significant change other than the depletion in acid precursor. There is ample bicarbonate, so that the loss of some is not soon felt. Furthermore in the presence of abundant glycogen and small quantities of glucose the spontaneous reaction which was responsible for the formation of "glucose phosphate" in the first place at once takes place again, restoring the quantity of acid precursor at the expense of some of the other two compounds. Except that it contains some sodium lactate the muscle is thus to all intents and purposes just where it was before being stimulated, and is able to respond to another stimulus virtually as well as before.

It is clear, however, that if stimulation is repeated continuously

the accumulation of sodium lactate will presently assume considerable proportions. A fundamental law of chemistry is that the products of a reaction must be removed if the reaction is to continue. It follows that as sodium lactate piles up the reaction between lactic acid and sodium bicarbonate is interfered with, and as that reaction lags the decomposition of "glucose phosphate" is hampered in turn. How these processes affect the behavior of the muscle is described in later paragraphs.

Recovery Oxidation. The above account of contraction in a muscle deprived of oxygen holds in every particular for one supplied with the gas; there is in the latter, however, an additional series of reactions by which the sodium lactate is got rid of. These reactions include oxidation processes, as can be proven both by the production of CO_2 and the evolution of heat, as well as by their failure to occur in muscles deprived of oxygen. The oxidations make energy available, and one of the very interesting examples of the economy of operation of the Body is afforded by the fact that these oxidations instead of merely destroying the sodium lactate, are utilized for saving it. The situation in brief is this: three means exist by which sodium lactate might be disposed of: the first is to allow it to diffuse out from the muscle tissue into the blood, be conveyed thence to the kidneys, and be eliminated along with other complex waste products; the second is to oxidize it, a process that would give rise to sodium bicarbonate, water, and carbon dioxid, two useful products, the third easily eliminated through the lungs (p. 448); the final means is to change the lactic acid portion of the lactate molecules back into glucose or glycogen so that it can be used over again. The first of these processes is both wasteful and injurious; injurious because accumulation of lactates in the blood is presumably responsible for the condition of general bodily fatigue (p. 121), and if all the lactates produced in muscular exercise had to stay in the blood until the kidneys could eliminate them we would suffer as much from slight exertion as we do now from severe, and would probably find it impossible to perform heavy muscular work on account of the great accumulation of lactates that would necessarily occur. The second process, *i. e.*, getting rid of the lactates by burning them, would be just as wasteful as the first and in addition would increase about fivefold the amount of heat produced in muscular exercise (see below).

As it is, the problem of disposing of the heat generated during muscular work is difficult enough in warm weather; if all the lactates had to be burned we would probably not be able to work hard in places of great heat; such tasks as require heavy toil at high temperatures would be impossible of performance. Both these difficulties are obviated in large measure, and at the same time the lactates are conserved to the Body, in the arrangement actually present, which is one whereby a moderate amount of fuel is burned and the energy thus made available is utilized to convert the lactates back into glucose or glycogen. It will be recalled that glucose (and its compound, "glucose phosphate") has a higher energy value than lactic acid, the energy of muscular action being supposed to be derived from the change of the first into the second. In order to change lactates back into glucose as much energy must be supplied from some source as was set free when the "glucose phosphate" was decomposed. As a matter of fact, although the amount of fuel burned yields only about one-fifth as much energy as would be set free if the lactates themselves were completely oxidized, there is still much more burned than necessary to furnish the theoretically required amount of energy. In other words, the muscles are inefficient, using the expression in the engineering sense (p. 110), and much heat is produced as a by-product of muscular action.

The question of *what fuel is burned* in the process of recovery oxidation is of some importance. There are three fuel substances known to be present, one or all of which might serve. First, there is sodium lactate itself, of which one-fifth might be burned, thus furnishing the necessary energy for the reconversion of the other four-fifths to glucose or glycogen; secondly, glucose itself may be oxidized; and thirdly, fats may serve as fuel. We have no means at present of knowing whether lactates or equivalent amounts of sugar are burned, since the end result is the same in either case, *i. e.*, the using up of definite amounts of the latter in performing given amounts of work; if lactates are burned, equivalent amounts of sugar must be changed into acid precursor; if no lactates are burned, and all are reconverted into precursor, a corresponding amount of glucose must be burned. There has been a difference of opinion among investigators as to whether muscles have the power to burn fats directly, or must first convert them into glucose.

There is no doubt that fats (or fat compounds) are taken up by muscle cells and utilized for fuel; if they are first converted into sugar there is a waste of about ten per cent of their fuel value in the process; some investigators have obtained figures indicating that this amount of waste occurs when muscles are forced to obtain their energy at the expense of fats. There is other evidence, to be presented later (p. 542), indicating strongly, on the other hand, that fats are oxidized as such. The point to bear in mind is that under normal conditions the energy by which muscular work is performed is obtained at the expense in the main of glucose, but also in part of fat.

Summary of the Contraction Process. The chemical events in a simple muscular twitch can be at once summarized and placed in their relation with the mechanical acts of contraction and relaxation by reference to figure 46 below. The main facts to be emphasized are that the sudden formation of lactic acid from its precursor results from stimulation, and in turn causes tension to be developed, and hence contraction to occur; that the reaction of lactic acid with sodium bicarbonate to form sodium lactate necessarily precedes and accompanies relaxation; and that the recovery oxidation can lag behind the other processes, since the muscle can both contract and relax efficiently for a time whether this oxidation takes place or not.

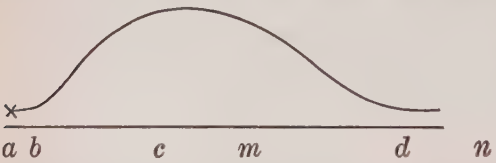


FIG. 46.—To indicate the sequence of chemical events in relation to the act of contraction. *a*, point of stimulation; *ab*, latent period; *ac*, period of conversion of "glucose phosphate" into lactic acid, and consequent acidification of the fibrillar surfaces; *cd*, period of conversion of lactic acid into sodium lactate, permitting relaxation; *mn*, period of recovery oxidation, usually much longer in proportion to other periods than indicated here.

The Beneficial Effect of Exercise. An interesting fact about skeletal muscle, that is in the experience of every athlete, and can also be demonstrated upon an isolated muscle, is that the response to stimulation after a period of inaction is less vigorous than the response to precisely the same amount of stimulation after the muscle has been exercised for a while. This fact probably explains in part the necessity under which baseball pitchers and other athletes labor of "warming up" before they can use their muscles

effectively, although the need of arousing an active circulation of blood plays a part also. In the case of an isolated muscle stimulated at regular intervals the effect is seen in a well-marked increase in the height of contraction during the first dozen or so of the series. This increase from contraction to contraction is often very regular, suggesting a flight of stairs. For this reason it is often spoken of as the "staircase phenomenon."

Fatigue of Muscle—Contracture. If an isolated muscle is subjected to a series of stimulations at fairly frequent intervals—one a second or oftener—the period of the "staircase" described above is usually followed by a period in which the *relaxation* of the muscle is definitely slowed. So far as can be seen the muscle *contracts* as rapidly and forcibly as ever, but the relaxations are drawn out. The effect of this in a regular series of stimulations is that the muscle fails to relax completely from one stimulation by the time the next one is sent in, so that it continues in a state

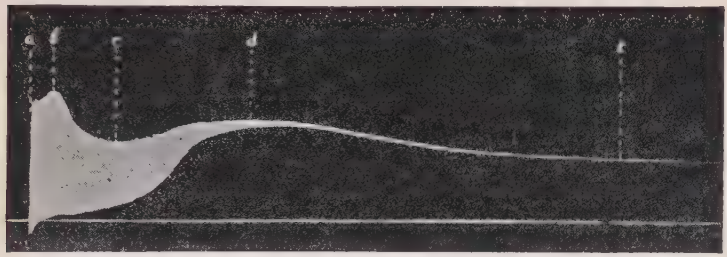


FIG. 47.—Record of contractions made on smoked paper by an isolated muscle (frog) stimulated five times per second. The contractions are fused because the kymograph was moving very slowly. *a-b*, period of "stair-case"; *c-d*, development of contracture.

of partial contraction during the intervals between stimulations. This condition is called *contracture*. It is shown graphically in figure 47. It consists essentially of a slowing down of the relaxation rate, and is the first indication of the condition of impairment that we call *fatigue*.

Both contracture and fatigue are explained as due to the accumulation of sodium lactate within the muscle fibers (p. 116). In an isolated muscle, even though not specially deprived of oxygen, the interior fibers are more or less cut off from access to the oxygen of the surrounding air. When stimuli are applied in fairly rapid succession, so that sodium lactate is formed rapidly,

not enough oxygen diffuses into these fibers for the recovery oxidation to keep pace with it. The slowing of relaxation (contracture) is obviously the result of the hampering of the reaction between lactic acid and sodium bicarbonate, by accumulating lactate, and the lessening in height of contraction (fatigue) the result of the diminution in conversion of "glucose phosphate" to lactic acid from the same cause (p. 116).

The Body can go into Debt for Oxygen. In the Body muscles receive their oxygen supply from the rapidly circulating blood, and accordingly are much more efficiently aërated than are isolated muscles. Notwithstanding this it is possible for the muscles in the Body to suffer from lack of oxygen. There are millions of individual muscle fibers, and when great exertion is performed a large percentage of them are in nearly continuous action. The amount of oxygen the muscles can receive per second is limited by the amount of blood that can flow through them in that time, as well as by the amount of oxygen present in the blood. This quantity is ample for resting muscles, and sufficient for muscles that are only moderately active; but when great numbers of fibers are at work all at once, and as nearly continuously as it is possible for muscle fibers to work (see below), sodium lactate is produced much faster than the amount of oxygen available will sustain the reaction by which it is reconverted into glucose. Under these circumstances the surplus lactate is disposed of by the first of the methods described on p. 116, *i. e.*, by dialyzing out into the blood. It is calculated that a powerful man can produce surplus lactates at the rate of three grams a second, and can keep on doing so until his Body contains 130 grams, or more than a quarter of a pound.

The lactates thus poured out do not all stay in the blood stream; the kidneys discharge some and still more dialyze back out of the blood into various inactive tissues. It is very exceptional for all the muscles in the Body to be active at once; probably this happens only during severe convulsions. Inactive muscles take up lactates that come to them in the blood stream and convert the same into glucose; as fast as reconversion takes place more lactates can be taken up, and the process continued. Furthermore, exertion so violent as to lead to this great outpouring of lactates can only be maintained for a short time; the active muscles presently become

inactive and now that they are no longer producing lactates can themselves take up lactates from the blood to be reconverted into glucose. This reconversion process is long drawn out. It can go only so fast as the blood can deliver oxygen to the tissues over and above their ordinary resting needs, for the "recovery oxidation" is a special process, distinct from basic metabolism. When amounts of lactates are produced approaching the figures given above about an hour and a half usually elapses before the Body is clear of them. While the energy for muscular activity is thus furnished ultimately by oxidation processes it is not necessary that the oxidation keep absolute pace with the muscular activity. The relationship is expressed by the saying that "the Body can go into debt for oxygen."

General Bodily Fatigue. The feeling of exhaustion that attends violent exertion is attributed to the presence of lactates in the blood, and by dialysis in the nervous tissues from which our sensations necessarily come. We can account for the fatigue that attends muscular exercise thus. It is not clear whether fatigue from severe mental labor, or the weariness that comes sooner or later from loss of sleep, even though no great amount of work is done, is due to lactates in blood and tissues or not. The details of metabolism are still too obscure for us to be able to say what chemical substances may cause sensations of weariness. A point whose significance will be discussed in a later chapter is that ordinary feelings of fatigue do not necessarily imply inability on the part of the muscles to do work; they indicate rather a falling off in the efficiency of action of certain nervous structures. The exhaustion resulting from the presence of excessive quantities of lactate in blood and tissues is, on the contrary, indication of actual inability of the muscles to function effectively. Not until the lactate has been removed can the muscles display their usual power.

The Response to Rapidly Repeated Stimuli. Tetanus. Since a simple muscular contraction occupies one-tenth of a second, it is obvious that a second stimulus following the first within that interval will find the muscle in a state of partial or complete contraction, depending on the exact length of the interval. In such a case the muscle executes in response to the second stimulus a second contraction, which is fused with the first. Similarly a third can

be elicited, which will be fused with the second, and so on. A series of such fused contractions is known as a *physiological tetanus*. If the interval between stimuli does not exceed $\frac{1}{10}$–$\frac{1}{12}$ of a second in fresh frog's muscle the fusion is complete. That is, there are no signs of relaxation between stimuli, and the contraction is perfectly steady. In human muscle the interval between stimuli must be somewhat less for complete fusion to occur.

The fusion of contractions in tetanus is not difficult to explain when we recall that each stimulus sets off a chain of reactions of which the first one is the conversion of just enough "glucose phosphate" into lactic acid to bring about the limiting degree of acidity (p. 115), and the second the combination of the acid thus produced with sodium bicarbonate to form sodium lactate. Likewise, accompanying the first reaction is an "equilibrium reaction" between glucose, glycogen, and "glucose phosphate" which promptly tends to restore the quantity of the latter to its original value. Even though stimuli follow each other in such rapid succession that "glucose phosphate" is converted into lactic acid as fast as or faster than the acid can react with bicarbonate to form lactate, the supply of available "glucose phosphate" is not soon used up. There is also no reason why recovery oxidation should not go on during tetanus, tending to prevent lactates from accumulating unduly. As a matter of fact, however, a muscle in tetanus squeezes its own blood vessels so nearly shut as to cut down its blood supply materially. Oxygen-lack consequently develops almost immediately, and the second channel described above for getting rid of surplus lactates, *i. e.*, by dialysis into the blood, is also closed. It follows that tetanus of a whole muscle cannot be sustained for more than a few seconds. Partial tetanus, in which only a few fibers are involved at one time, can be sustained much longer, since blood can flow through the portions of the muscle where the fibers are inactive, and experiment shows that in partial tetanus the fibers work in relays, one set after another taking up the burden.

An interesting fact about physiological tetanus, or *tetanic contraction* as it is often called, is that the *extent* of the contraction may be markedly greater than in a simple contraction, even though the latter may have been maximal. Evidently the so-called maximal simple contraction is not maximal in the sense that it represents the mechanical limit of the muscle's power to shorten,

but only in that it is the utmost the muscle can do in response to a single stimulus. In two respects, then, the tetanic contraction differs from the simple twitch: in being more prolonged, and in being higher.

Voluntary Muscular Contraction. In view of the superiority of the tetanus over the simple twitch it is interesting to note that all voluntary muscular movements, even the briefest, are tetanic in character. They owe this special character to a peculiarity of the nervous system, through which the muscles are excited to contract. When nerve-cells discharge their impulses into muscles the discharge is never a single one but always a series in rapid succession. The result in the muscle is, of course, a tetanus.

The Electrical Phenomena of Muscle. When a living muscle is carefully exposed and suitable electrodes connected with a sensitive galvanometer or electrometer are applied to its surface the entire surface is found to be isoelectric, *i. e.*, having a uniform electric potential. If, however, an injury such as cutting or burning is inflicted upon any part of the muscle the injured surface is found to possess a different potential from the surrounding uninjured surfaces. This difference of potential is shown by movements of the indicator of the galvanometer or electrometer. These movements are usually in such a direction as to indicate that the injured region has a lower potential than uninjured parts of the same tissue. This difference of potential existing between injured and uninjured living tissue is often referred to as the *current of injury*, although no current actually flows unless the two regions are connected by an electrical conductor. No current of injury can be obtained by connecting living tissue with dead tissue. Only while the injured tissue is in act of dying does it exhibit the altered potential which may give rise to an injury current.

The explanation of the change of electric potential accompanying an injury to living tissue is found in the fact that the death process which follows injury involves extensive chemical changes in the tissue. This disturbance in chemical relationship brings about corresponding disturbance in the electric equilibrium which finds expression in an altered electric potential in the part where the chemical activity is going on.

Just as the chemical changes which follow injury to the tissue give rise to the change of electrical potential which we call the

current of injury, so the chemical changes which accompany normal activity in the tissue give rise to electrical changes which are designated *currents of action*. Action currents cannot easily be demonstrated in an ordinary contracting muscle because the whole muscle goes into contraction at once and so the electric potential of its entire surface rises and falls uniformly. In the heart we have a muscle, however, which does not contract all at once, the contraction sweeping over it from base to apex. The action currents of the heart, therefore, can be demonstrated without difficulty if the apparatus used for detecting them is able to respond quickly enough to recurrent changes of potential in opposite directions. Delicate galvanometers have been devised which answer admirably for the purpose. Another interesting method of demonstrating the action currents of the heart is by causing them to act as stimuli for an irritable tissue. If in a recently killed frog the sciatic nerve is dissected out as far as the knee and cut away from its connection with the spinal cord, being left in connection with the leg below, and if this nerve is laid on the exposed beating heart of the same frog or some other recently killed animal, often the muscles of the lower leg and foot which are connected with the nerve will contract at each beat of the heart. The nerve where it lies on the heart serves as a conductor for the action currents as they are generated in the heart, and the action currents in turn stimulate the nerve during their flow through it.

Physiology of Smooth Muscle. Smooth muscle differs strikingly from skeletal muscle, not only, as stated previously, in structure, but also in mode of action. Aside from the fact that both sorts of muscle produce their effects by contraction they have almost no features in common. Weight for weight smooth muscle is much less powerful than skeletal muscle. Its movements are also much slower. Smooth muscle constitutes the operating machinery of the maintenance systems (except the respiratory system), and it is as nicely adjusted to the special requirements of these systems as is skeletal muscle to the needs of external adaptation. One striking peculiarity of smooth muscle tissue is illustrated by the bladder. This organ sometimes contains a large amount of urine, at other times there is little or none in it. When the bladder is empty it is shrunken to a fraction of its size when

full. The muscular walls are distended or contracted as the organ is full or empty. These pronounced changes appear to be effected, in part at least, by rearrangement of the cells which make up the muscle coats. When the organ is distended the individual cells overlap only at their ends, while in the contracted bladder they may lie side by side for nearly their whole length. Just how this rearrangement is brought about is not known.

Another feature in which smooth muscle differs strikingly from skeletal is in the tendency it often shows to carry on spontaneous contractions. Skeletal muscle, as previously emphasized, contracts only when subjected to definite stimulation. Smooth muscle, on the other hand, often undergoes periods of rhythmic contraction and relaxation when no obvious sources of stimulation are present.

Still another peculiarity of smooth muscle is its ability to remain indefinitely in the contracted state without fatigue. This property is seen in the muscular coats of the small arteries, many of which are never relaxed. They may be more strongly contracted at some times than at others but in health they are always in some degree of contraction.

There are in the body a number of sphincters, circular bands of smooth muscle which guard the openings of various organs such as the stomach, large intestine, and bladder. These are strongly contracted the greater part of the time, relaxation being for them only an occasional occurrence. They maintain their condition of strong contraction without fatigue and apparently without much expenditure of energy, offering in this regard a sharp contrast to skeletal muscle.

To excite skeletal muscle sharp stimuli, like the electric shock, are most efficient. Smooth muscle, on the other hand, responds best to slower, more prolonged excitants. A pull or pinch, which will ordinarily fail to cause contraction in such a muscle as the gastrocnemius, arouses a strip of stomach muscle to pronounced activity.

Mechanism of Contraction of Smooth Muscle. The structure of smooth muscle is, as shown formerly, much less complex than of skeletal muscle. No elaborate system of fibrils, sarcoplasm, and sarcolemma exists. The spindle-shaped cells with their environment of tissue fluid are the contractile elements. In fact when we attempt to compare smooth muscle with skeletal we find that the

smooth muscle-cell corresponds better to the fibril than to the fiber, although the fiber is the cell unit. The tissue fluid which bathes the cell of smooth muscle functions toward it as does the sarcoplasm toward the fibril. Contraction of smooth muscle depends, then, on interaction of muscle-cell with tissue fluid as in skeletal muscle on interaction of fibril with sarcoplasm. This latter interaction is of such a sort that to keep the fibrils in a state of tension a continuous expenditure of energy is necessary, and fatigue is bound ultimately to occur. The expenditure of energy in smooth muscle, on the other hand, appears to take place only during an actual change in length, whether the change is a shortening or a lengthening; the maintenance of a given length after it is once attained seems not to require further energy liberation. This difference accounts for the ability of smooth muscle to continue in contraction without fatigue.

The suggestion made above, that energy expenditure occurs during change in length in smooth muscle, even though the change be a relaxation, is in harmony with the interesting fact that most smooth muscle tissues are supplied with two sets of nerves. Stimulation by way of one set induces contraction; by way of the other, relaxation. This is in marked contrast with the situation in skeletal muscle, where the only function of stimulation is to arouse contraction; relaxation following spontaneously upon the release from excitation.

Physiology of Cardiac Muscle. In some features of its activity heart muscle resembles skeletal muscle; in others it is more like smooth muscle. The contraction of heart muscle is rapid and vigorous, in this respect corresponding to skeletal muscle. The liberation of energy in heart muscle is associated with *contraction* rather than with change in length as such. Here again the resemblance is with skeletal muscle rather than with smooth.

Cardiac muscle is like smooth muscle in that it has the power of executing spontaneous contractions. The heart receives, also, the double innervation referred to above as characteristic of smooth muscle.

In a number of important regards the heart differs from either of the other types of muscle. For convenience discussion of these special features is deferred to the section in which the heart is studied as an organ of the circulation (Chap. XX).

CHAPTER VIII

THE USE OF MUSCLES IN THE BODY

The Special Physiology of the Skeletal Muscles. Having now considered separately the structure and properties in general of the skeleton, the joints, and the muscles, we may go on to consider how they all work together in the Body. Although the properties of muscular tissue are everywhere the same, the uses of different muscles are very varied, by reason of the different parts with which they are connected. Some are muscles of respiration, others of deglutition; many are known as *flexors* because they bend joints, others as *extensors* because they straighten them. The exact use of any particular muscle, acting alone or in concert with others, is known as its *special physiology*, as distinguished from its *general physiology*, or properties as a muscle without reference to its use as a muscle in a particular place. The functions of those muscles forming parts of the physiological mechanisms concerned in breathing and swallowing will be studied hereafter; for the present we may consider the muscles which co-operate in maintaining postures of the Body; in producing movements of its larger parts with reference to one another; and in producing *locomotion* or movement of the whole Body in space.

In nearly all cases the striated muscles carry out their functions with the co-operation of the skeleton, since nearly all are fixed to bones at each end, and when they contract primarily move these, and only secondarily the soft parts attached to them. To this general rule there are, however, exceptions. The muscle for example which lifts the upper eyelid and opens the eye arises from bone at the back of the orbit, but is inserted, not into bone, but into the eyelid directly; and similarly other muscles arising at the back of the orbit are directly fixed to the eyeball in front and serve to rotate it on the pad of fat on which it lies. Many facial muscles again have no direct attachment whatever to bones, as for example the muscle (*orbicularis oris*) which surrounds the mouth-opening, and by its contraction narrows it and purses out

the lips; or the *orbicularis palpebrarum* which similarly surrounds the eyes and when it contracts closes them.

Levers in the Body. When the muscles serve to move bones the latter are in nearly all cases to be regarded as levers whose fulcra lie at the joint where the movement takes place. Examples of all the three forms of levers recognized in mechanics are found in the Human Body.

Levers of the First Order. Examples of the first form of lever (fulcrum between power and weight, Fig. 48), are not numerous in the Human Body. One is afforded in the nodding movements of

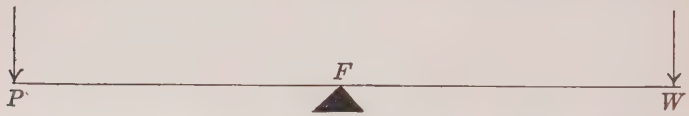


FIG. 48.—A lever of the first order. *F*, fulcrum; *P*, power; *W*, resistance or weight.

the head, the fulcrum being the articulations between the skull and the atlas. When the chin is elevated the power is applied to the skull, behind the fulcrum, by small muscles passing from the vertebral column to the occiput; the resistance is the excess in the weight of the part of the head in front of the fulcrum over that behind it, and is not great. To depress the chin as in nodding does not necessarily call for any muscular effort, as the head will fall forward of itself if the muscles keeping it erect cease to work, as those of us who have fallen asleep during a dull discourse on a hot day have learnt. If the chin, however, be depressed forcibly, as in the athletic feat of suspending one's self by the chin, the muscles passing from the chest to the skull in front of the occipital condyles are called into play. Another example of the employment of the first form of lever in the Body is afforded by the curtsey frequently taught to children. In curtseying the trunk is bent forward at the hip-joints, which form the fulcrum; the weight is that of the trunk acting as if all concentrated at its center of gravity, which lies a little above the sacrum and behind the hip-joints; and the power is afforded by muscles passing from the thighs to the front of the pelvis.

Levers of the Second Order. As an example of the employment of such levers (weight between power and fulcrum, Fig. 49)

in the Body, we may take the act of standing on the toes. Here the foot represents the lever, the fulcrum is at the contact of its fore part with the ground; the weight is that of the Body acting

FIG. 49.—A lever of the second order. *F*, fulcrum; *P*, power; *W*, weight. The arrows indicate the direction in which the forces act.

down through the ankle-joints at *Ta*, Fig. 33; and the power is the great muscle of the calf acting by its tendon inserted into the heel-bone (*Ca*, Fig. 33). Another example is afforded by holding up the thigh when one foot is kept raised from the ground, as in hopping on the other. Here the fulcrum is at the hip-joint, the power is applied at the kneecap by a great muscle (*quadriceps femoris*) which is inserted there and arises from the pelvis; and the weight is that of the whole lower limb acting at its center of gravity, which lies somewhere in the thigh between the hip and knee-joints, that is, between the fulcrum and the point of application of the power.

Levers of the Third Order. These are the levers most commonly used on the Human Body (power between weight and fulcrum, Fig. 50). For example, when the arm is bent at the elbow the fulcrum is the elbow-joint, the power is applied at the insertion of the biceps muscle (Fig. 37) into the radius and of

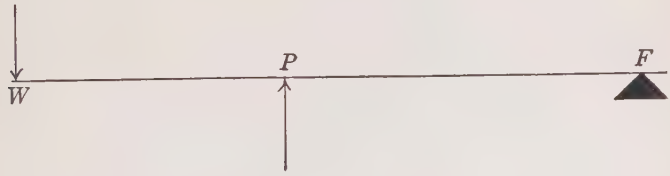


FIG. 50.—A lever of the third order. *F*, fulcrum; *P*, power; *W*, weight.

another muscle (not represented in the figure, the *brachialis anticus*,) into the ulna, and the weight is that of the forearm and hand, with whatever may be contained in the latter, acting at

the center of gravity of the whole somewhere on the distal side of the point of application of the power. In the Body the power-arm is usually very short so as to gain speed and range of movement, the muscles being powerful enough to do their work in spite of the mechanical disadvantage at which they are placed. The limbs are thus made much more shapely than would be the case were the power applied near or beyond the weight.

It is of course only rarely that simple movements like those described above take place. In the great majority several or many muscles co-operate.

The Loss to the Muscles from the Direction of their Pull. It is worthy of note that, owing to the oblique direction in which the muscles are commonly inserted into the bones, much of their force is lost so far as producing movement is concerned. Suppose the log of wood in the diagram (Fig. 51) to be raised by pull-

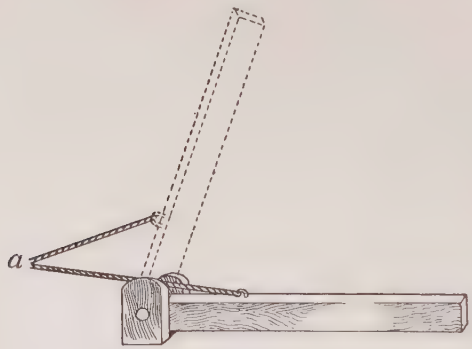


FIG. 51.—Diagram illustrating the disadvantage of an oblique pull.

ing on the rope in the direction *a;* it is clear at first that the rope will act at a great disadvantage; most of the pull transmitted by it will be exerted against the pivot on which the log hinges, and only a small fraction be available for elevating the latter. But the more the log is lifted, as for example into the position indicated by the dotted lines, the more useful will be the direction of the pull, and the more of it will be spent on the log and the less lost unavailingly in merely increasing the pressure at the hinge. If we now consider the action of the biceps (Fig. 37) in flexing the elbow-joint, we see similarly that the straighter the joint is, the more of the pull of the muscle is wasted. Beginning with the arm

straight, it works at a great disadvantage, but as the forearm is raised the conditions become more and more favorable to the muscle. Those who have practiced the gymnastic feat of raising one's self by bending the elbows when hanging by the hands from a horizontal bar know practically that if the elbow-joints are quite straight it is very hard to start; and that, on the other hand, if they are kept a little flexed at the beginning the effort needed is much less; the reason being of course the more advantageous direction of traction by the biceps in the latter case.

Experiment proves that the power with which a muscle can contract is greatest at the commencement of its shortening, the very time at which, we have just seen, it works at most mechanical disadvantage; in proportion as its force becomes less the conditions become more favorable to it. There is, however, it is clear, nearly always a considerable loss of power in the working of the skeletal muscles, strength being sacrificed for variety, ease, rapidity, extent, and elegance of movement.

The Equilibrium of Opposing Muscles. The muscles are highly elastic bodies, and on account of their elasticity exert, even while not actively contracting, a definite elastic tension upon their points of insertion. We have, therefore, at every joint, constant opposing pulls of the resting muscles. The efficient manner in which the elastic tensions of opposing muscles balance each other is often very striking, particularly when one considers the marked differences in size and in mechanical advantage apt to exist in opposing muscles. Take, for example, the muscles which move the fore arm. The flexor muscle (biceps) is a larger and stronger muscle than the extensor (triceps). It has, moreover, a better leverage. Yet so far as elastic tension is concerned the two muscles balance perfectly. One appreciates best the significance of this equilibrium when a case is seen in which it has been lost. The disease known as infantile paralysis injures or destroys the nervous connections of the skeletal muscles, and often affects one group while leaving the opposing group unimpaired. The normal tension is lost in the affected muscles but persists in the unaffected ones. Unless special precautions are taken to prevent the occurrence, the muscles which still exert elastic tension will gradually shorten, pulling the joint into the position into which it is drawn by the normal contractions of these muscles, and holding it there per-

manently, and so forcibly that extreme measures must often be adopted to return the part to its normal resting situation. The importance of this constant tension during life is probably in the instant readiness it gives the muscles. There is never any slack to be taken up; motion of the joint is simultaneous with the contraction of the muscle.

Functional Muscle Groups. In attempting to analyze the exceedingly numerous and diverse muscular movements of which we are capable we have to bear in mind that in the state of nature for which our bodies were primarily adapted men's movements were directed to fewer and simpler ends. Our fundamental activities fall into a small number of groups, and we shall see that our more complex movements are but modifications of the fundamental ones.

According to this principle we can classify our muscular acts as follows: *posture; locomotion; prehension* (grasping); *mastication* (and swallowing); *vision; voice production* (including breathing). Of these groups posture, locomotion, and prehension are treated in following paragraphs. A separate chapter is devoted to voice production (Chap. XXXIII). The others are treated in detail in connection with the discussion of the particular bodily functions with which they are associated. Some points of general interest concerning them may not be out of place here. Among the facial muscles are found groups devoted to mastication; to vision; to voice production; and to prehension. The masticatory and visual muscles do not show in man any very striking differences from their functioning in other mammals. Prehension, which in man and the higher monkeys is taken over so largely by the front limbs, manifests itself among the facial muscles in the grasping power of the very flexible lips, which are in most of the lower mammals important grasping organs, but in man confined chiefly to the safe guidance of food into the mouth.

The *tongue* is a muscular mass composed of several distinct muscles which are interwoven in such a manner that by their interaction they can draw, thrust, or twist the organ into the numerous positions and shapes it is capable of taking. The larger tongue muscles have a bony attachment at one end, either in the hyoid bone (p. 72) or the lower jaw. Their insertions are within the fleshy mass itself. There are besides these large muscles a number

of smaller ones which are imbedded wholly within the tongue. These have no bony attachments at either end.

In addition to its masticatory function (p. 496) the tongue is an essential part of the speech apparatus. Its importance is shown not only by the loss of the power of articulate speech from paralysis or removal of the tongue, but also by the fact that only those lower forms which have tongues at once fleshy and flexible (parrots, tongue-cut crows) can learn to talk. The ape's tongue is very similar to that of man. The fact that the parrot can learn to talk while the ape cannot, or will not, raises the interesting question in connection with the lower animals as to how much speech depends on tongue-structure and how much on intelligence or willingness to imitate sounds. The solution of this problem is a matter for the student of animal behavior rather than for the physiologist.

Postures. The term posture is applied to those positions of equilibrium of the Body which can be maintained for some time, such as standing, sitting, or lying, compared with leaping, running, or falling. In all postures the condition of stability is that the vertical line drawn through the center of gravity of the Body shall fall within the basis of support afforded by objects with which it is in contact; and the security of the posture is proportionate to the extent of this base, for the wider it is the less is the risk of the perpendicular through the center of gravity falling outside of it on slight displacement.

The Erect Posture. This is pre-eminently characteristic of man, his whole skeleton being modified with reference to it. Nevertheless the power of maintaining it is only slowly learnt in the first years after birth, and for a long while it is unsafe. And though finally we learn to stand erect without conscious attention, the maintenance of that posture always requires the co-operation of many muscles, co-ordinated by the nervous system. The influence of the latter is shown by the fall which follows a severe blow on the head, which may nevertheless have fractured no bone nor injured any muscle: the concussion of the brain, as we say, "stuns" the man, and until its effects have passed off he cannot stand upright. In standing with the arms straight by the sides and the feet together the center of gravity of the whole adult Body lies in the articulation between the sacrum and the last lumbar vertebra, and the perpendicular drawn from it will reach the ground

between the two feet, within the basis of support afforded by them. With the feet close together, however, the posture is not very stable, and in standing we commonly make it more so by slightly separating them so as to increase the base. The more one foot is in front of the other the more swaying back and forward will be compatible with safety; and the greater the lateral distance separating them the greater will be the lateral sway which is possible without falling. Consequently we see that a man about to make great movements with the upper part of his Body, as in fencing or boxing, or a soldier preparing for the bayonet exercise, always commences by thrusting one foot forward obliquely, so as to increase his basis of support in both directions.

The ease with which we can stand is largely dependent upon the way in which the head is almost balanced on the top of the vertebral column, so that but little muscular effort is needed to keep it upright. In the same way the trunk is almost balanced on the hip-joints, but not quite, its center of gravity falling rather behind them; so that just as some muscular effort is needed to keep the head from falling forwards, some is needed to keep the trunk from toppling backwards at the hips. In a similar manner other muscles are called into play at other joints: as between the vertebral column and the pelvis, and at the knees and ankles; and thus a certain rigidity, due to muscular effort, extends all along the erect Body: which, on account of the flexibility of its joints, could not otherwise be balanced on its feet, as a statue can. Beginning (Fig. 52) at the ankle-joint, we find it kept stiff in standing by the combined and balanced contraction of the muscles passing from the heel to the thigh, and from the dorsum of the foot to the shin-bone (*tibia*). Others passing before and behind the knee-joint keep it from yielding; and so at the hip-joints: the others again, lying in the walls of the abdomen and along the vertebral column, keep the latter rigid and erect on the pelvis; and finally the skull is kept in position by muscles passing from the sternum and vertebral column to it, in front of and behind the occipital condyles.

Posture the Task of the Extensor Muscles. In the maintenance of posture the muscles which bear the strain are in general the *extensors*, since posture requires that the joints shall be kept from bending. So far as the flexors co-operate they do so by preventing overextension, a part which calls for relatively little exer-

tion. The degree of pull manifested by the extensor muscles in the maintenance of posture is slight but steady. In the course of a day we may become aware of postural fatigue, showing that muscular activity has been present, although we may not have been conscious of definite volition. This mild degree of sustained contraction, which differs strikingly from the ordinary rapid and extensive contractions of skeletal muscle, is known as *tonus*. In the maintenance of posture it is chiefly *extensor tonus*. Tonus is looked upon as a highly co-ordinated partial tetanus (p. 121.) Just as many fibers are thrown into contraction as necessary to sustain the action. Before these develop fatigue the stimulation shifts to another set, and so on around and around, each group of fibers in the muscle taking its turn in due order.

FIG. 52.—Diagram illustrating the muscles (drawn in thick black lines) which pass before and behind the joints and by their balanced activity keep the joints rigid and the body erect.

Locomotion includes all the motions of the whole Body in space, dependent on its own muscular efforts: such as walking, running, leaping and swimming.

Walking. In walking the Body never entirely quits the ground, the heel of the advanced foot touching the ground in each step before the toe of the rear foot leaves it. The advanced limb supports the Body, and the foot in the rear at the commencement of each step propels it.

Suppose a man standing with his heels together to commence to walk, stepping out with the left foot: the whole Body is at first inclined forwards, the movement taking place mainly at the ankle-joints. By this means the center of gravity would be thrown in front of the base formed by the feet and a fall on the face result, were not simultaneously the left foot slightly raised by bending the knee and then swung forwards, the toes just clear of the ground, and, in good walking the sole nearly parallel to it. When the step is completed the left knee is straightened and the sole placed on

the ground, the heel touching it first, and the base of support being thus widened from before back, a fall is prevented. Meanwhile the right leg is kept straight, but inclines forwards along with the trunk when the latter advances, and as this occurs the sole gradually leaves the ground, commencing with the heel. When the step of the left leg is completed the great toe of the right alone is in contact with the support. With this a push is given which sends the trunk on over the left leg, which is now kept rigid, except at the ankle-joint; and the right knee being bent that limb swings forwards, its foot just clearing the ground as the left did before. The Body is meanwhile supported on the left foot alone, but when the right completes its step the knee of that leg is straightened and the foot thus placed, heel first, on the ground. Meanwhile the left foot has been gradually leaving the ground, and its toes only are at that moment upon it: from these a push is given, as before, with the right foot, and the knee being bent so as to raise the foot, the left leg swings forwards at the hip-joint to make a fresh step.

During each step the whole Body sways up and down and also from side to side. It is highest at the moment when the advancing trunk is vertically over the foot supporting it, and then sinks until the moment when the advancing foot touches the ground, when it is lowest. From this moment it rises as it swings forward on this foot, until it is vertically over it, and then sinks again until the other touches the ground; and so on. At the same time, as its weight is alternately transferred from the right to the left foot and *vice versa*, there is a slight lateral sway, commonly more marked in women than in men, and which when excessive produces an ugly "waddling" gait.

The length of each step is primarily dependent on the length of the legs; but can be controlled within wide limits by special muscular effort. In easy walking little muscular work is employed to carry the rear leg forwards after it has given its push. When its foot is raised from the ground it swings on, like a pendulum; but in fast walking the muscles passing in front of the hip-joint, from the pelvis to the limb, by their contraction forcibly carry the leg forwards. The easiest step, that in which there is most economy of labor, is that in which the limb is let swing freely, and since a short pendulum swings faster than a longer, the natural step of short-legged people is quicker than that of long-legged ones.

In fast walking the advanced or supporting leg also aids in propulsion; the muscles passing in front of the ankle-joint contracting so as to pull the Body forwards over that foot and aid the push from the rear foot. Hence the fatigue and pain in front of the shin which is felt in prolonged, very fast walking. From the fact that each foot reaches the ground heel first, but leaves it toe last, the length of each stride is increased by the length of the foot.

Running. In this mode of progression there is a moment in each step when both feet are off the ground, the Body being unsupported in the air. The toes alone come in contact with the ground at each step, and the knee-joint is not straight when the foot reaches the ground. When the rear foot is to leave the support, the knee is suddenly straightened, and at the same time the ankle-joint is extended so as to push the toes forcibly on the ground and give the whole Body a powerful push forwards and upwards. Immediately after this the knee is greatly flexed and the foot raised from the ground, and this occurs before the toes of the forward foot reach the latter. The swinging leg in each step is violently pulled forwards and not suffered to swing naturally, as in walking. By this the rapidity of the succession of steps is increased, and at the same time the stride is made greater by the sort of one-legged leap that occurs through the jerk given by the straightening of the knee of the rear leg just before it leaves the ground.

Leaping. In this mode of progression the Body is raised completely from the ground for a considerable period. In a powerful leap the ankles, knees, and hip-joints are all flexed as a preparatory measure, so that the Body assumes a crouching attitude. The heels, next, are raised from the ground and the Body balanced on the toes. The center of gravity of the Body is then thrown forwards, and simultaneously the flexed joints are straightened, and by the resistance of the ground, the Body receives a propulsion forwards; much in the same way as a ball rebounds from a wall. The arms are at the same time thrown forwards. In leaping backwards, the Body and arms are inclined in that direction; and in jumping vertically there is no leaning either way and the arms are kept by the sides.

Prehension. In man, and to a less extent in monkeys, the fore limbs are differentiated from organs of locomotion into pre-

hensile structures. To a large degree the effectiveness of the fore limb as an organ of prehension depends on peculiarities of its bony framework. These have been described in detail in a previous chapter (p. 77). The chief special features, which it may not be amiss to recall, are three: the attachment of the shoulder girdle to the trunk by muscles rather than by a firm bony articulation; the rotation of the radius over the ulna; the opposibility of the thumb to each of the fingers. These skeletal features, which afford a groundwork for great flexibility of action, are made effective by the arrangement of the arm muscles. Although detailed description of this arrangement is outside the scope of this work, some general statements may properly be presented.

The muscles of the arm fall into three groups, shoulder muscles, muscles of the upper arm, muscles of the fore arm and hand. The muscles of the shoulder are arranged so that the arm can be raised or lowered; drawn forward or backward. Those at the back of the shoulder include within their mass the shoulder blade (*scapula*) in such a manner that in ordinary upward movements of the arm the rotation is about the shoulder joint, but in extensive upward movements, as in raising the arms above the head, the shoulder blade itself is pulled out of its ordinary horizontal position into a nearly vertical one.

The muscles of the upper arm are simple flexors and extensors since the elbow-joint is a hinge-joint, permitting no variety of movements. The muscles of the fore arm and hand have a great variety of movements to provide for, and are accordingly numerous and complicated. Only the arrangements for securing flexion and extension will be mentioned here. The front of the fore arm is made up of a number of muscles, of which most are flexors of the wrist or of the fingers. Similarly the back of the fore arm contains the extensors of wrist and of fingers. The tendons of the latter muscles form the conspicuous cords at the back of the hand. These flexors and extensors interact in an interesting fashion. Thus the flexors of the finger aid in flexion of the wrist. If flexion of the fingers without accompanying flexion of the wrist is desired the latter must be prevented by simultaneous contraction of the wrist extensors. Similarly the extensors of the fingers act also to extend the wrist. To secure extension of the fingers while the wrist is flexed the latter position must be maintained

by activity of the wrist flexor to overcome the tendency of the finger extensors to extend the wrist.

Hygiene of the Muscles. The healthy working of the muscles needs of course a healthy state of the Body generally, so that they shall be supplied with proper materials for growth and repair, and have their wastes rapidly and efficiently removed. In other words, good food and pure air are necessary for a vigorous muscular system, a fact which trainers recognize in insisting upon a strict dietary, and in supervising generally the mode of life of those who are to engage in athletic contests. The muscles should also not be exposed to any considerable continued pressure, since this interferes with the flow of blood and lymph through them.

As far as the muscles themselves are directly concerned, exercise is the necessary condition of their best development. The muscles are so compactly built that the movement of blood and lymph through them is less free than in other tissues. During rhythmic contractions and relaxations, however, the circulation both of blood and of lymph is augmented by the recurrent pressure of the muscle upon its own contents. For their proper nourishment most of the muscles are largely dependent upon this self-massage. A muscle which is permanently unused suffers serious impairment of nutrition, and usually degenerates and is absorbed, little finally being left but the connective tissue of the organ and a few muscle-fibers filled with oil-drops. This is well seen in cases of paralysis dependent on injury to the nerves. In such cases the muscles may themselves be perfectly healthy at first, but lying unused for weeks they become altered, and finally, when the nervous injury has been healed, the muscles may be found incapable of functional activity. The physician therefore is often careful to avoid this by exercising the paralyzed muscles daily by means of electrical shocks sent through the part; passive exercise, as by proper massage, is frequently of great use in such cases. The same fact is illustrated by the feeble and wasted condition of the muscles of a limb which has been kept for some time in splints. After the latter have been removed it is only slowly, by judicious and persistent exercise, that the long-idle muscles regain their former size and power. The great muscles of the "brawny" arm of the blacksmith or wrestler illustrate the reverse fact, the growth of the muscles by exercise. We may note, incidentally, that in

this growth from exercise there is no increase in the *number* of muscle-fibers. The greater size is due to growth of the individual fibers. Exercise, to be effective, must be judicious; repeated frequently to the point of exhaustion it does harm; the period of repair is not sufficient to counteract the injurious effects of fatigue, and the muscles thus waste under too violent exercise as with too little. Rest should alternate with work, and that regularly, if benefit is to be obtained. Moreover, violent exercise should never be suddenly undertaken by one unused to it, not only lest the muscles suffer, but because muscular effort greatly increases the work of the heart. No general rule can be laid down as to the amount of exercise to be taken; for a healthy man in business the minimum would perhaps be represented by a daily walk of five miles.

Varieties of Exercise. In walking and running the muscles chiefly employed are those of the lower limbs and trunk. This is in part true of rowing, which when good is performed much more by the legs than the arms; especially when sliding seats are used. Hence any of these exercises alone is apt to leave the muscles of the chest and arms imperfectly exercised. Indeed, no one exercise employs equally or proportionately all the muscles: therefore gymnasia in which various feats of agility are practiced, so as to call different parts into play, have very great utility. It should be borne in mind, however, that the legs especially need strength; while the upper limbs, in which delicacy of movement, as a rule, is more desirable than power, do not require so much exercise; and the fact that gymnastic exercises are commonly carried on indoors is a great drawback to their value. When the weather permits, out-of-door exercise is far better than that carried on in even the best ventilated and lighted gymnasium. For those who are so fortunate as to possess a garden there is no better exercise, at suitable seasons, than an hour's daily digging in it; since this calls into play nearly all the muscles of the Body; while of games, lawn tennis is perhaps the best from a hygienic view that has ever been invented, since it not only demands great muscular agility in every part of the Body, but trains the hand to work with the eye in a way that walking, running, rowing and similar pursuits do not. For the same reasons baseball, cricket, golf and boxing are excellent.

Exercise in Infancy and Childhood. Young children have not only to strengthen their muscles by exercise, but also to learn to use them. Watch an infant trying to convey something to its mouth, and you will see how little control it has over its muscles. On the other hand, the healthy infant is never at rest when awake; it constantly throws its limbs around, grasps at all objects within its reach, coils itself about, and so gradually learns to exercise its powers. It is a good plan to leave every healthy child more than a few months old several times daily on a large bed, or even on a rug or carpeted floor, with as little covering as is safe, and that as loose as possible, and let it wriggle about as it pleases. In this way it will not only enjoy itself thoroughly, but gain strength and a knowledge of how to use its limbs. To keep a healthy child swathed all day in tight and heavy clothes is cruelty.

When a little later the infant commences to crawl it is safe to permit it to as much as it wishes, but unwise to tempt it to do so when disinclined: the bones and muscles are still feeble and may be injured by too much work. The same is true of learning to walk.

From four or five to twelve years of age almost any form of exercise should be permitted, or even encouraged. During this time, however, the epiphyses of many bones are not firmly united to their shafts, and so anything tending to throw too great a strain on the joints should be avoided. After that up to commencing manhood or maidenhood any kind of outdoor exercise for healthy persons is good, for girls as well as for boys.

Exercise in Youth should be regulated to a certain extent by sex; not that women are to be shut up and made pale, delicate, and unfit to share the duties or participate fully in the pleasures of life; but the other calls on the strength of the young woman render vigorous muscular work often unadvisable, especially under conditions where it is apt to be followed by a chill.

A healthy boy or young man may do nearly anything; but until twenty-two or twenty-three very prolonged effort is unadvisable. The frame is still not firmly knit or as capable of endurance as it will subsequently become.

Girls should walk, ride, row or play outdoor games in moderation; with enough supervision to insure that the strength is not overtaxed, but otherwise with as much freedom as is allowed to boys.

Exercise in Adult Life. Up to forty a man may carry on safely the exercises of youth, but after that sudden efforts should be avoided. A lad of twenty-one or so may, if trained, safely run a quarter-mile race, but to a man of forty-five it would be dangerous, for with the rigidity of the cartilages and blood vessels which begins to show itself about that time comes a diminished power of meeting a sudden violent demand. On the other hand, the man of thirty would more safely than the lad of nineteen or twenty undertake a marathon run; the prolonged effort would be less dangerous to him, though the tax on both strength and endurance is greater than any except the most vigorous can meet safely. Probably for one engaged in active business a walk of two or three miles to it in the morning and back again in the afternoon is the best and most available daily exercise. Golf is a pleasant and valuable form. The chief objection to it as the sole form, as it is tending more and more to become, is that it usually has to be confined to the week-ends, leaving the intervening days almost devoid of exercise.

For women during middle life the same rules apply: there should be some regular but not violent daily exercise.

In Old Age the needful amount of exercise is less, and it is still more important to avoid sudden or violent effort.

Exercise for Invalids. This should be regulated under medical advice. For feeble persons gymnastic exercises are especially valuable, since from their variety they permit of selection according to the condition of the individual; and their amount can be conveniently controlled.

Training. If any person attempt some unusual exercise he soon finds that he loses breath, gets perhaps a "stitch in the side," and feels his heart beating with unwonted violence. If he persevere he will probably faint—or vomit, as is frequently seen in the case of imperfectly trained men at the end of a hard boat-race. These phenomena are avoided by careful gradual preparation known as "training." The immediate cause of them lies in disturbances of the circulatory and respiratory organs, on which excessive work is thrown.

CHAPTER IX

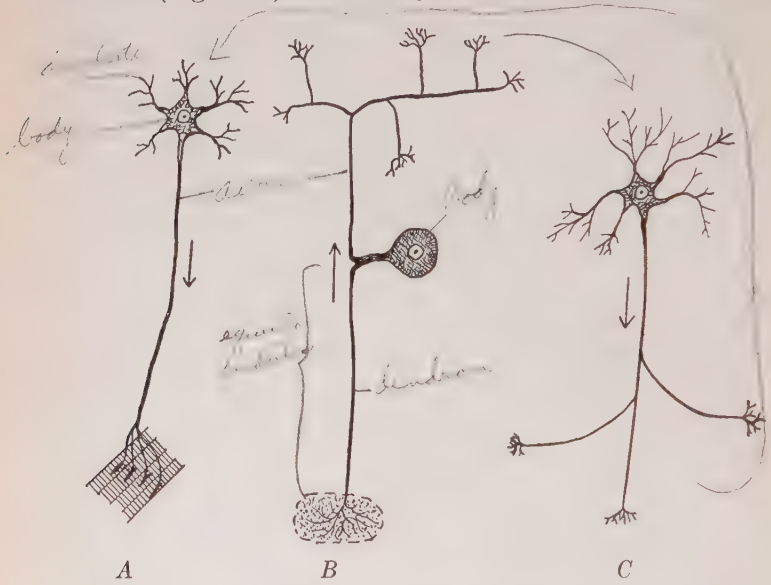
ANATOMY OF THE NERVOUS SYSTEM

General Statement. In Chapter III the special function of the nervous system was outlined, and was shown to involve the transmission of stimuli from the sensory regions of the Body to the active tissues (muscles and glands), and in the course of such transmission to make whatever modifications are necessary to the production of the best results. The sensory regions of the Body are numerous; there are likewise many muscles. Successful adaptation of the individual to his surroundings may call at one time or another for the passage of stimuli from any sensory region to any muscle, or for the combination of stimuli from several sensory regions to form stimuli to go to any group of muscles. A somewhat analogous situation occurs in the telephone systems which are such important features of modern life. In these communication may be desired between any pair of instruments in the system. To make this possible all the telephones in any one system are led into a central exchange where provision is made for connecting any instrument with any other. Flexibility of communication between sensory and motor regions in the Body is secured in somewhat similar fashion. All nerves from sensory regions are led into a central "exchange" from which start all nerves to the motor organs.

Nerve Impulses. Since it is impossible to describe the nervous system without frequent reference to the messages which nerves carry it is desirable before proceeding further to state that it has become the custom to call these messages *nerve impulses.* When we speak of a nerve impulse we have in mind the process by which the message is transmitted along the nerve. The situation corresponds to that in a telephone wire. When the latter is transmitting a message the words spoken into the transmitter are not carried along, but an electrical disturbance which they set up. So the nerve does not transmit the exact stimulus which acts upon it, but a nerve impulse which the stimulus arouses. The characteristics of nerve impulses are stated in the next chapter.

Neurons. The nervous system as a whole is made up of structures called neurons, each of which is a single nerve cell.

A typical neuron consists of a *cell-body* containing a nucleus and from whose surface project many rather short branching processes called *dendrites*, and a single long process having usually only a few branches and known as the *axon* (Fig. 55). Neurons which convey impulses to muscles (*motor neurons*) have this structure (Fig. 53*A*). The only branching of a motor neuron



A *B* *C*

FIG. 53.—Types of neurons. *A*, motor; *B*, sensory; *C*, internuncial.

is at its very end, where it is distributed to the muscle fibers of which it has control. The number of muscle fibers thus innervated by one motor neuron varies in different muscles, ranging from a half dozen to fifty or more.

The neurons which convey impulses from sensory regions to the center (*sensory neurons*) have a structure which appears at first view to be altogether different from that of the typical neuron just described. They have cell-bodies with nuclei but instead of a single axon and numerous much-branched dendrites the cell-body gives rise to two long axon-like processes, one connecting with the receptor and known as a *dendron*, and the other which is

the true axon, having a number of branches. The *bipolar* character of these neurons, moreover, is concealed in many through the union of the two processes for a short distance from the cell-body, giving an appearance as though the latter were on a side branch of a long axon (Fig. 53*B*). The underlying similarity of these to the type neuron appears if we consider that the dendrites of the typical neuron are replaced in the sensory neuron by the dendron which connects with the receptor.

A third sort of neurons occurring in the Body resembles the first or motor type in the possession of cell-body and many branching dendrites. Instead of long, slightly branched axons, however, neurons of this sort have short and very much-branched ones. These neurons occur interposed in the pathway of impulses from sensory to motor neurons and are called *internuncial* or connecting neurons (Fig. 53*C*): they are not, however, the only sort of internuncial neurons; many neurons which belong physiologically to this group in that they form communicating paths between sensory and motor neurons are anatomically of the type to which all motor neurons belong.

Since each single neuron represents one nerve-cell, neurons are the largest cells known. Although axons are so small in cross-section as to be microscopic they may have a length of three feet or more, as in the nerve-trunks which extend down the legs to the feet.

The nervous system as a whole is made up of neurons of these three types. The sensory neurons, as stated above, lead from the receptors to the center; motor neurons lead from the center to the active tissues; and internuncial neurons form the connecting links wherever such are necessary. All sensory neurons communicate with other neurons at their central terminations. Since the central axons are branched (see above) each sensory neuron has a number of such connections. All motor neurons have likewise connections with other neurons at their central ends. Internuncial neurons connect with other neurons at both ends, as they must if they are to serve as links in a chain whose ends are sensory and motor neurons.

Synapses. Communication between neuron and neuron is always according to a certain scheme. The axons of all except motor neurons end in masses of fine branches known as *end arbori-*

zations. These are in contact with the branching dendrites of some other neuron. The surfaces of contact between the end arborization of one neuron and the dendrites of another constitute what is called a *synapse.* In order for a nerve impulse to pass from one neuron to another it must cross this synapse.

The Myelin Sheath. All true nerve tissue has a characteristic gray color. This statement applies equally to cell-bodies, dendrites, and axons. Most, but not all, of the long axons of the body are inclosed within sheaths composed chiefly of a substance, *myelin,* which has a characteristic glossy white color. The myelin sheath where present does not inclose the axon throughout its entire length; near the cell-body and again near its termination the axon is not inclosed. Surrounding the myelin sheath, or, where it is absent, the axon itself, is a delicate membrane, the *neurilemma.* The myelin sheath is made up of short segments which are separated one from another by the *nodes of Ranvier.*

The myelin sheath is not composed of living cells and so does not contain nuclei. The neurilemma, however, is a living membrane; scattered along it at intervals are nuclei. The function of the myelin sheath is not known. Perhaps the most satisfactory suggestion that has been offered is that it serves as an insulator to keep the nerve impulse within its own axon and prevent its escape to adjacent ones.

Axons which are inclosed in myelin sheaths are spoken of as *medullated* or myelinated nerve-fibers.

It is the presence of myelin sheaths that gives to certain parts of the nervous system their characteristic white appearance. All "white matter" is made up of medullated axons. "Gray matter," on the other hand, is made of cell-bodies and dendrites, together with some nonmedullated axons.

The Central and Peripheral Nervous Systems. In a preceding paragraph was pointed out the analogy between the nervous system and a telephone system. That part of the nervous system corresponding to the telephone "exchange," to which sensory neurons lead and from which motor neurons spring is called the *central nervous system.* It consists of the *brain* and *spinal cord.* (The analogy between the central nervous system and a telephone exchange should not be pushed too far, for the central nervous system has numerous functions in addition to the simple one of

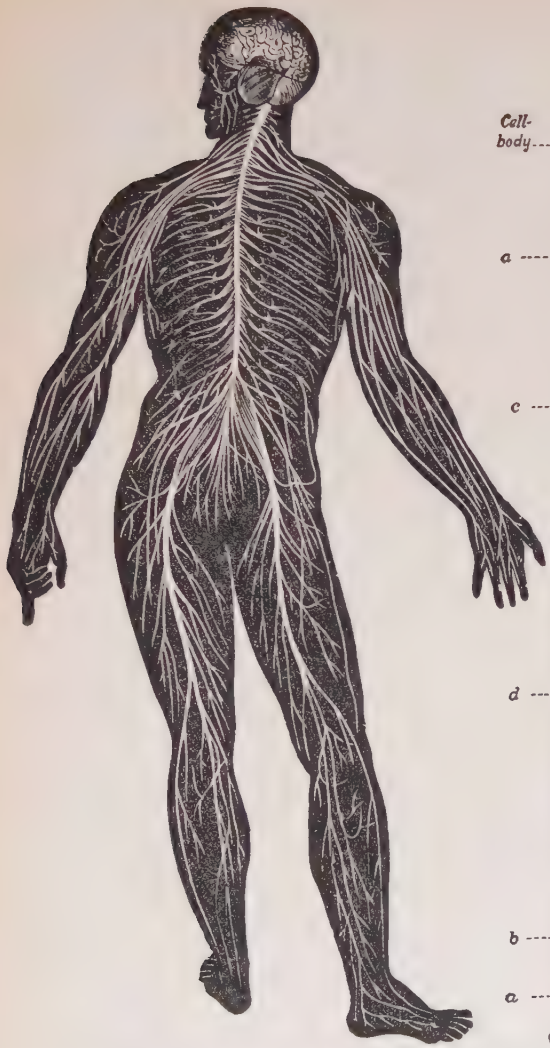


FIG. 54.—Diagram illustrating the general arrangement of the nervous system.

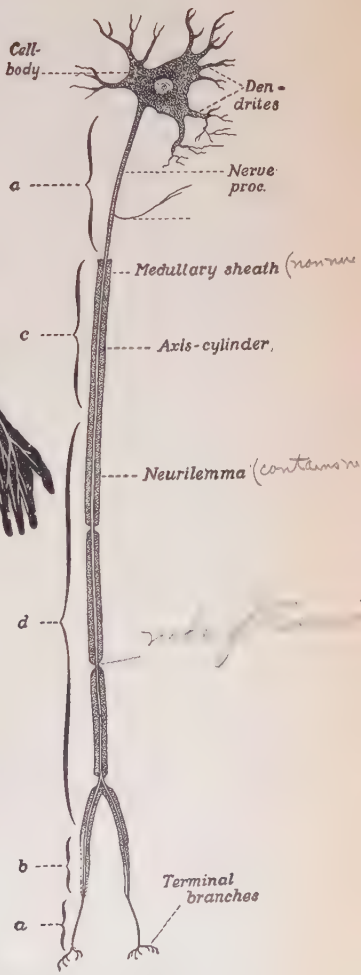


FIG. 55.—Diagram of neuron (*Stohr.*)

making connections between sensory and motor neurons. These special functions have to do with the modification of the impulses passing through it for the best advantage of the organism as a whole.)

Springing from the central nervous system and corresponding to the cables bearing wires to individual telephones are forty-three pairs of nerve-trunks. Twelve pairs arise from the brain and are called *cranial nerves;* the remaining thirty-one pairs arise from the spinal cord and are called *spinal nerves.* Each nerve-trunk contains a large number of axons, and in most nerve-trunks both the axons of motor and the dendrons of sensory neurons are present. These forty-three pairs of nerve-trunks with their ramifications to all parts of the Body constitute the *peripheral nervous system* (Fig. 54).

There are in the Body a set of neurons which though part of the peripheral nervous system are specially adapted for a certain function and are therefore usually considered independently. These constitute the *sympathetic* or *autonomic system.*

The Central Nervous System and its Membranes. Lying inside the skull is the *brain* and in the neural canal of the vertebral column the *spinal cord,* the two being continuous through the *foramen magnum* of the occipital bone. The central nervous system is bilaterally symmetrical throughout except for slight differences on the surfaces of parts of the brain, which are often found in the higher races of mankind. Both brain and spinal cord are very soft and easily crushed; nervous tissue as well as the connective tissue and a peculiar supporting tissue (*neuroglia*) which pervades it being delicate; accordingly both organs are placed in nearly completely closed bony cavities and are also enveloped by membranes which give them support. These membranes, known collectively as the *meninges,* are three in number. Externally is the *dura mater,* very tough and strong and composed of white fibrous and elastic connective tissues. In the cranium the dura mater adheres by its outer surface to the inside of the skull chamber, serving as the periosteum of its bones; this is not the case in the vertebral column, where the dura mater forms a loose sheath around the spinal cord and is only attached here and there to the surrounding bones, which have a separate periosteum of their own. At certain places in the cranium the dura is folded to form

two layers; between these layers is a space, known as a *sinus*, communicating with the veins of the region, and forming part of the channel through which venous blood flows. The innermost membrane lies in immediate contact with the proper nervous parts. This is the *pia mater*, also made up of white fibrous tissue interwoven with elastic fibers, but less closely than in the dura mater, so as to form a less dense and tough membrane. The pia mater contains many blood vessels which break up in it into small branches before entering the nervous mass beneath. Immediately underlying the dura mater is a layer of flat closely fitting cells, making up the third membrane, called the *arachnoid*. In the space between the arachnoid and the pia mater, the so-called *sub-arachnoid* space, is contained a small quantity of watery *cerebrospinal liquid*. The pia follows the folds of the brain; the dura and arachnoid stretch across from one to another; there is accordingly quite a sub-arachnoid space in the region of the folds.

Ventricles of the Brain and Central Canal of the Spinal Cord. The central nervous system begins its embryonic development as a groove in the layer of cells which forms the upper surface of the embryro. This groove deepens, and finally cuts itself off from the cell layer of which it was at first a part. The edges grow together transforming the groove into a tube. The cell layer heals over, leaving the *neural tube* beneath it. The hollow in the tube persists throughout life. In the adult spinal cord it is represented by the tiny central canal (Fig. 65). As the front end of the neural tube develops into the complex brain the hollow in this region takes the form of a series of chambers of extremely irregular shape, communicating with each other and with the central canal of the spinal cord by narrow channels. The chambers are four in number, and are known as the *ventricles* of the brain. There is one in each cerebral hemisphere (p. 153). These are called the *lateral ventricles*. Numerically they rank as first and second. The lateral ventricles open into a narrow chamber in the base of the cerebrum in the mid line, known as the third ventricle. This in turn communicates by a narrow channel (the aqueduct of Sylvius) with the cavity of the brain stem (p. 154) which is called the fourth ventricle.

The cavity of the fourth ventricle communicates with the arachnoid space by three small openings in its roof, one in the

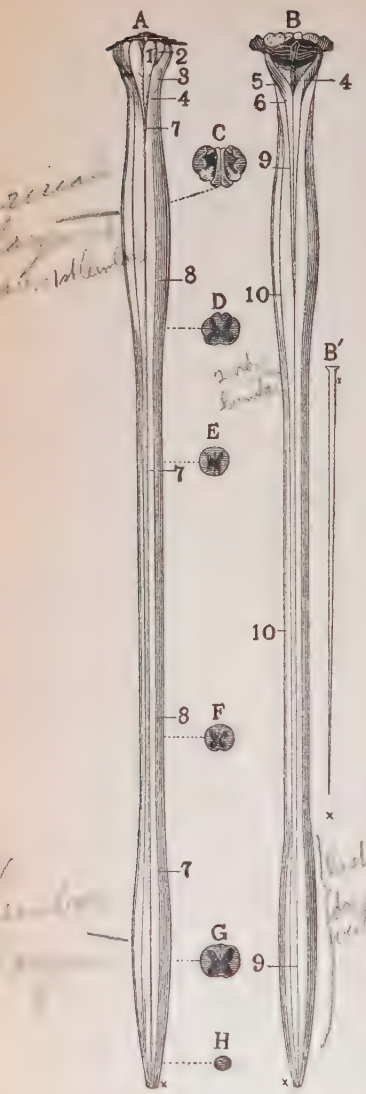


FIG. 56.—The spinal cord and *medulla oblongata*. *A*, from the ventral, and *B*, from the dorsal aspect; *C* to *H*, cross-sections at different levels.

mid line and one at each lateral border. By these openings the cerebrospinal fluid which occupies the arachnoid space is continuous with that which fills the ventricles and central canal.

Cerebrospinal Fluid. This fluid, which occupies all the spaces within and around the central nervous system, is in general similar to the tissue fluid by which the other tissues of the body are bathed (p. 308). It presents some chemical differences, however, which become accentuated in certain diseases. In the lumbar region there is room between the processes of the vertebræ so that a hypodermic needle can be thrust into the arachnoid space and some of the cerebrospinal fluid withdrawn. The operation is simple and by the application of cocaine to the skin made virtually painless. Chemical examination of the fluid so obtained is often helpful in diagnosing obscure complaints.

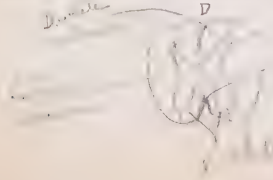
The source of the fluid is in vascular structures within the ventricles, the *choroid plexuses*; from these cerebrospinal fluid is continuously separated at such a rate as to yield about 200 cubic centimeters (nearly a half pint) every twenty-four hours. The fluid passes out of the ventricles into the sub-arachnoid space by way of the minute openings in the roof of the fourth ventricle. From the sub-arachnoid space it is reabsorbed into the blood. If any one of the openings between one ventricle and another becomes occluded as by disease, fluid accumulates within the ventricles thus cut off from their normal outlet. The result-

ing pressure upon the delicate nervous structures is disastrous. In young children the accumulation of fluid distends the head far beyond its normal size, giving the condition known as "hydrocephalus."

The Spinal Cord (Fig. 56) is nearly cylindrical in form, being however a little wider from side to side than dorsiventrally, and tapering off at its posterior end. Its average diameter is about 19 millimeters (¾ inch) and its length 0.43 meter (17 inches). It weighs 42.5 grams (1½ ounces). There is no marked limit between the spinal cord and the brain, the one passing gradually into the other (Fig. 62), but the cord is arbitrarily said to commence opposite the outer margin of the foramen magnum of the occipital bone: from there it extends to the articulation between the first and second lumbar vertebræ, where it narrows off to a slender non-nervous filament, the *filum terminale* (cut off and represented separately at B^1 in Fig. 56, which runs back to the end of the neural canal behind the sacrum. In its course the cord presents two expansions, an upper, 10, the *cervical enlargement*, reaching from the third cervical to the first dorsal vertebræ, and a lower or *lumbar enlargement*, 9, opposite the last dorsal vertebra.

Running along the middle line on both the ventral and the dorsal aspects of the cord is a groove, and a cross-section shows that these grooves are the surface indications of fissures which extend deeply into the cord (*C*, Fig. 57) and nearly divide it into right and left halves.

The *ventral fissure* (1, Fig. 57) is wider and shallower than the *dorsal*, 2, which indeed is hardly a true fissure, being completely filled up by an ingrowth of pia meter. The transverse section, *C*, shows also that the substance of the cord is not alike throughout, but that its *white* superficial layers envelop a central *gray substance* arranged somewhat in the form of a capital H. Each half of the gray matter is crescent-shaped, and the crescents are turned back to back and united across the middle line by the *gray commissure*. The tips of each crescent are called its horns or *cornua*, and the *ventral horn* on each side is thicker and larger than the dorsal. In the cervical and lumbar enlargements the proportion of white to gray matter is greater than elsewhere; and as the cord approaches the medulla oblongata its central gray mass becomes irregular in form and begins to break up into smaller



portions. If lines be drawn on the transverse section of the cord from the tip of each horn of the gray matter to the nearest point of the surface, the white substance in each half will be divided into three portions: one between the ventral fissure and the ventral cornu, and called the *ventral white column;* one between the dorsal fissure and the dorsal cornu, and called the *dorsal white column;* while the remaining one lying in the hollow of the crescent and

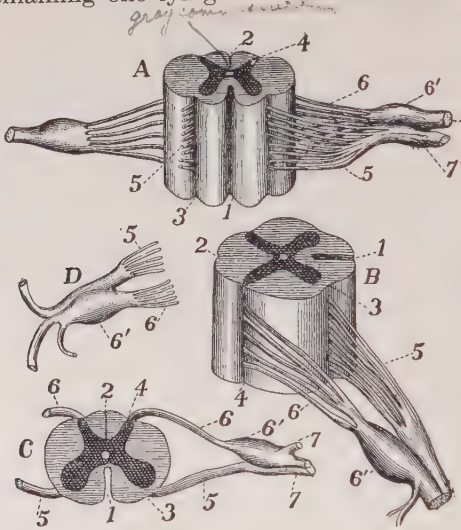


Fig. 57.—The spinal cord and nerve-roots. *A*, a small portion of the cord seen from the ventral side; *B*, the same seen laterally; *C*, a cross-section of the cord; *D*, the two roots of a spinal nerve; 1, ventral fissure; 2, dorsal fissure; 3, surface groove along the line of attachment of the ventral nerve-roots; 4, line of origin of the dorsal roots; 5, ventral root filaments of spinal nerve; 6, dorsal root filaments; 6′, ganglion of the dorsal root; 7, 7′, the first two divisions of the nerve-trunk after its formation by the union of the two roots. The grooves are much exaggerated.

between the two horns is the *lateral column:* the ventral and lateral columns of the same side are frequently named the *ventrolateral column.* A certain amount of white substance crosses the middle line at the bottom of the ventral fissure; this forms the *ventral white commissure.* There is no dorsal white commissure, the bottom of the dorsal fissure being the only portion of the cord where the gray substance is uncovered by white. Running along the middle of the gray commissure, for the whole length of the cord, is the *central canal,* previously described. It is a tiny channel just visible to the unaided eye.

The Brain (Fig. 58) is far larger than the spinal cord and more complex in structure. It weighs on the average about 1,415 grams (50 ounces) in the adult male, and about 1,260 grams (44.5 ounces) in the female. In its simpler forms the vertebrate brain consists of three masses, each with subsidiary parts, following one another in series from before back, and known as the fore-brain, midbrain, and hind-brain respectively. In man the fore-brain,

FIG. 58.—Diagram illustrating the general relationships of the parts of the brain. *A*, fore-brain; *b*, midbrain; *B*, cerebellum; *C*, pons Varolii; *D*, medulla oblongata; *B*, *C*, and *D* together constitute the hind-brain.

A, weighing about 1,245 grams (44 ounces), is much larger than all the rest put together and laps over them behind. It consists mainly of two large convoluted masses, separated from one another by a deep median fissure, and known as the *cerebral hemispheres*. The immense proportionate size of these is very characteristic of the human brain. Beneath each cerebral hemisphere is an *olfactory bulb*, inconspicuous in man but in some animals larger than the cerebral hemispheres. Buried in the fore-brain on each side are two large gray masses, the *corpora striata* and *optic thalami*. The midbrain forms a connecting isthmus between the two other divisions and presents on its dorsal side four hemispherical eminences, the *corpora quadrigemina* or *colliculi*. On its ventral side it exhibits two semicylindrical pillars (seen under the nerve *IV* in Fig. 62), known as the *crura cerebri*. The hind-

brain consists of three main parts: on its dorsal side is the cerebellum, *B* (Fig. 58), consisting of a *right*, a *left*, and a *median lobe;* on the ventral side is the *pons Varolii, C* (Fig. 58), and behind that the *medulla oblongata, D* (Fig. 58), which is continuous with the spinal cord. The medulla and midbrain together make up the *brain stem.*

In nature, the main divisions of the brain are not separated so much as has been represented in the diagram for the sake of clear-

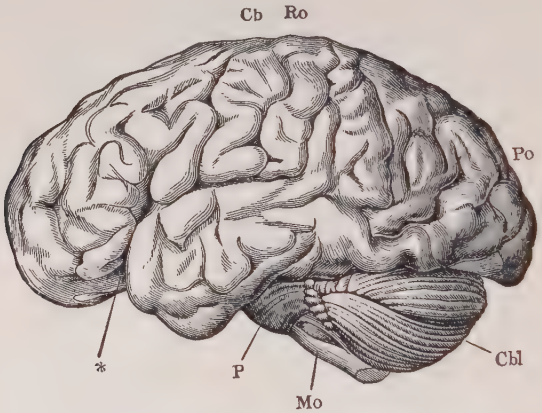


FIG. 59.—The brain from the left side. *Cb*, the cerebral hemispheres forming the main bulk of the fore-brain; *Cbl*, the cerebellum; *Mo*, the medulla oblongata; *P*, the pons Varolii; *, the lateral sulcus or fissure of Sylvius; *Ro*, the central sulcus or fissure of Rolando; *Po*, the Parieto-occipital fissure.

ness, but lie close together, as represented in Fig. 59, only some folds of the membranes extending between them; and the midbrain is entirely covered in on its dorsal aspect. Nearly everywhere the surface of the brain is folded, the folds, known as *gyri* or *convolutions*, being deeper and more numerous in the brain of man than in that of the animals nearest allied to him; and in the human species more marked in the higher than in the lower races. It should however be added that some species of animals which are not markedly intelligent have much convoluted cerebral hemispheres.

The brain, like the spinal cord, consists of gray and white nervous matter, but somewhat differently arranged, for while the brain, like the cord, contains gray matter in its interior, a great part of its surface is also covered with it. By the external convolutions

of the cerebellum and the cerebral hemispheres the surface over which this gray substance is spread is very much increased (see Fig. 59).

The Spinal Nerves. Thirty-one pairs of spinal nerve-trunks enter the neural canal of the vertebral column through the intervertebral foramina (p. 67). Each divides in the foramen into a dorsal and ventral portion known respectively as the *dorsal* and *ventral roots* of the nerve (6 and 5, Fig. 57), and these again

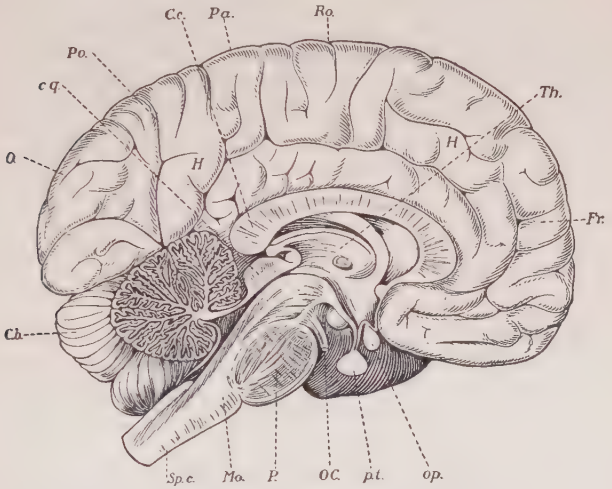


FIG. 60.—Diagram of the left half of a vertical median section of the brain (Sobotta-McMurrich, *Atlas and Text-book of Human Anatomy*). *H*, *H*, convoluted inner surface of left cerebral hemisphere; *Cc*, corpus callosum; *Th*, optic thalamus; *c.q.*, corpora quadrigemina; *Cb*, cerebellum; *Sp.c*, spinal cord; *Mo*. medulla oblongata; *P*, pons Varolii; *oc*, oculo-motor nerve; *pt*, pituitary body; *op*, optic nerve; *Ro*, central sulcus (fissure of Rolando); *Po*, parieto-occipital fissure; *Fr*, frontal lobe; *Pa*, parietal lobe; *O*, occipital lobe.

subdivide into finer branches which are attached to the sides of the cord, the dorsal root at the point where the dorsal and lateral white columns meet, and the ventral root at the junction of the lateral and ventral columns. Although the nerve-trunks contain both sensory and motor neurons these are completely separated in the roots; the dorsal root contains only sensory neurons; the ventral only motor. At the lines on which the roots are attached there are superficial furrows on the surface of the cord. On each dorsal root is a *spinal ganglion* (6′, Fig. 57), placed just before

it joins the ventral root to make up the common nerve-trunk. This spinal ganglion contains the cell-bodies of the bipolar sensory neurons. Immediately after its formation by the mixture of fibers from both roots, the trunk divides (*D*, Fig. 57), into a *dorsal primary*, a *ventral primary*, and a *communicating branch*. The branches of the first set go for the most part to the skin and muscles on the back; from the second arise the nerves for the sides and ventral region of the neck and trunk and for the limbs; the communicating branches form part of the autonomic system.

The various spinal nerves are named from the portions of the vertebral column through the intervertebral openings of which they pass out; and as a general rule each nerve is named from the vertebra in front of it. For example, the nerve passing out between the fifth and sixth thoracic vertebræ is the "fifth thoracic" nerve, and that between the last thoracic and first lumbar vertebræ, the "twelfth thoracic." In the cervical region, however, this rule is not adhered to. The nerve passing out between the occipital bone and the atlas is called the "first cervical" nerve, that between the atlas and axis the second, and so on; that between seventh cervical and first thoracic vertebræ being the "eighth cervical" nerve. The thirty-one pairs of spinal nerves are therfore thus distributed: 8 cervical, 12 thoracic, 5 lumbar, 5 sacral, and 1 coccygeal; the latter passing out between the sacrum and coccyx. Since the spinal cord ends opposite the upper lumbar vertebræ while the sacral and coccygeal nerves pass out from the neural canal much farther back, it is clear that the roots of those nerves, on their way to unite in the foramina of exit and form nerve-trunks, must run obliquely backwards in the spinal canal for a considerable distance. One finds in fact the neural canal in the lumbar and sacral regions, behind the point where the spinal cord has tapered off to form the *filum terminale*, occupied chiefly by a great bunch of nerve-roots forming the so-called "horse's tail" or *cauda equina*.

Plexuses. Very frequently several neighboring nerve-trunks send off communicating branches to one another, each branch carrying fibers from one trunk to the other. Such networks are called *plexuses* (Fig. 61), and through the interchanges taking place in them it often happens that the distal branches of a nerve-

trunk contain fibers which it does not possess as it leaves the central nervous system.

Distribution of the Spinal Nerves. It would be out of place here to go into detail as to the exact portions of the Body sup-

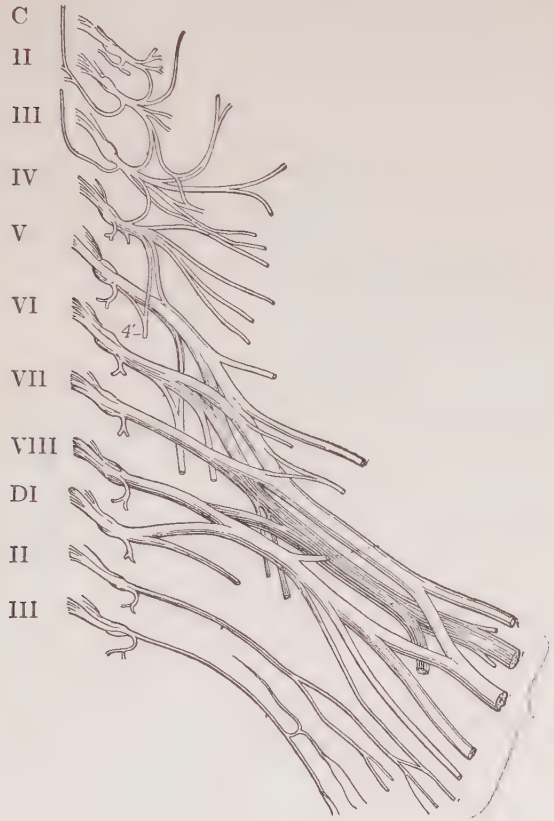


FIG. 61.—The cervical and brachial plexuses of the left side of the Body.

plied by each spinal nerve, but the following general statements may be made. The ventral primary branches of the first four cervical nerves form on each side the *cervical plexus* (Fig. 61) from which branches are supplied to the muscles and skin of the neck: also to the outer ear and the back part of the scalp. The

ventral primary branches of the remaining cervical nerves and the first dorsal form the *brachial plexus*, from which the upper limb is supplied. The roots of the trunks which form this plexus arise from the cervical enlargement of the spinal cord.

From the fourth and fifth cervical nerves on each side, small branches arise and unite to make the *phrenic nerve* (4′, Fig. 61) which runs down through the chest and ends in the diaphragm.

The ventral primary branches of the thoracic nerves, except part of the first which enters the brachial plexus, form no plexus, but each runs along the posterior border of a rib and supplies branches to the chest-walls, and the lower ones to those of the abdomen also.

The ventral primary branches of the four anterior lumbar nerves are united by branches to form the *lumbar plexus*. It supplies the lower part of the trunk, the buttocks, the front of the thigh, and inner side of the leg.

The *sacral plexus* is formed by the ventral primary branches of the fifth lumbar and the first four sacral nerves, which unite in one great cord and so form the *sciatic nerve*, which is the largest in the Body and, running down the back of the thigh, ends in branches for the lower limb. The roots of the trunks which form the sacral plexus arise from the lumbar enlargement of the cord.

Cranial Nerves. Twelve pairs of nerves leave the skull by apertures in its base, and are known as the cranial nerves. Most of them spring from the under side of the brain, and so they are best studied in connection with the base of that organ, which is represented in Fig. 62. The *first pair*, or *olfactory nerves*, spring from the under sides of the olfactory bulbs, *I*, and pass out through the roof of the nose. They are the nerves of smell. The *second pair*, or *optic nerves*, *II*, spring from the optic thalami and corpora quadrigemina, and, under the name of *optic tracts*, run down to the base of the brain, where they appear passing around the crura cerebri, as represented in the figure. In the middle line the two optic tracts unite to form the *optic chiasma*, from which an optic nerve proceeds to each eyeball.

All the remaining cranial nerves arise from the hind-brain. The *third pair* (*oculomotor*) arise from the front of the pons Varolii, and are distributed to most of the muscles which move the eyeball and also to that which lifts the upper eyelid.

The *fourth pair* of nerves (*trochlear*) *IV*, arise from behind the crura cerebri. From there, each curls around a *crus cerebri* (the cylindrical mass seen beneath it in the figure, running from the pons Varolii to enter the under surface of the cerebral hemispheres)

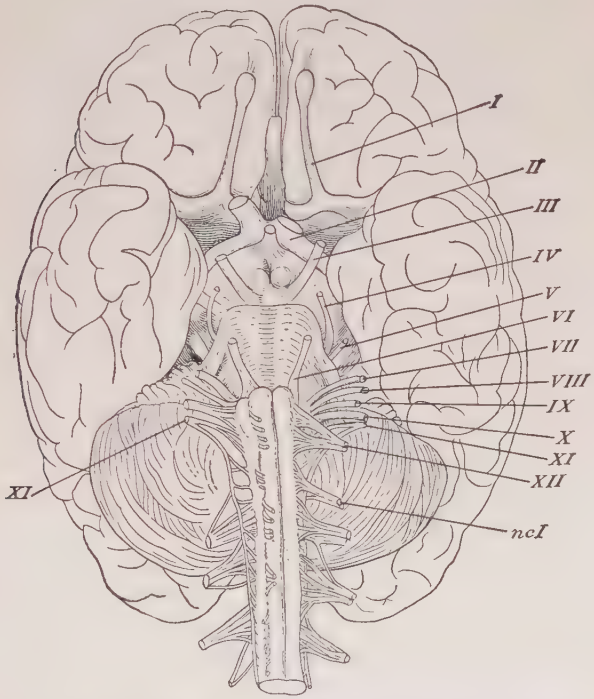


FIG. 62.—The base of the brain. The cerebral hemispheres are seen overlapping all the rest. *I*, olfactory bulbs; *II*, optic tract passing to the optic chiasma from which the optic nerves proceed; *III*, the third nerve or *oculomotor; IV*, the fourth nerve or *trochlear; V*, the fifth nerve or *trigeminalis; VI*, the sixth nerve or *abducens; VII*, the seventh or *facial* nerve; *VIII*, the *acoustic* nerve; *IX*, the ninth or *glossopharyngeal; X*, the tenth or *vagus; XI*, the *accessory; XII*, the *hypoglossal; ncI*, the first cervical spinal nerve.

and appears on the base of the brain. Each goes to one muscle of the eyeball.

The *fifth pair* of nerves (*trigeminales*), *V*, resemble the spinal nerves in having two roots; one of these is much larger than the other and possesses a ganglion (the *Gasserian* or *semilunar ganglion*) like the dorsal root of a spinal nerve. Beyond the ganglion the two roots form a common trunk which divides into three

main branches. Of these, the *ophthalmic* is the smallest and is mainly distributed to the muscles and skin over the forehead and upper eyelid; but also gives branches to the mucous membrane lining the nose, and to the integument over it. The second division (*maxillary*) of the trigeminal gives branches to the skin over the temple, to the cheek between the eyebrow and the angle of the mouth, and to the upper teeth; as well as to the mucous membrane of the nose, pharynx, soft palate and roof of the mouth. The third division (*mandibular*) is the largest branch of the trigeminal; it receives some fibers from the larger root and all of the smaller. It is distributed to the side of the head and the external ear, the lower lip and lower part of the face, the mucous membrane of the mouth and the anterior two-thirds of the tongue, the lower teeth, the salivary glands, and the muscles which move the lower jaw in mastication.

The *sixth pair* of cranial nerves *VI*, or *abducentes* arise from the posterior margin of the pons Varolii, and each is distributed to one muscle of the eyeball.

The *seventh pair* (*facial nerves*), *VII*, appear also at the posterior margin of the pons. They are distributed to most of the muscles of the face and scalp.

The *eighth pair* (*acoustic nerves*), *VIII*, arise close to the facial. They are the nerves of hearing and are distributed entirely to the internal ear.

The *ninth pair* (*glossopharyngeals*), *IX*, arising close to the acoustics, are distributed to the mucous membrane of the pharynx, the posterior part of the tongue, and the middle ear.

The *tenth pair* (*vagus nerves*), *X*, arise from the sides of the medulla oblongata. Each gives branches to the pharynx, gullet, and stomach, the larynx, windpipe, and lungs, and to the heart. The vagus runs farther through the Body than any other cranial nerve.

The *eleventh pair* (*accessory nerves*), *XI*, do not arise mainly from the brain but by a number of roots attached to the lateral columns of the cervical portion of the spinal cord, between the ventral and dorsal roots of the proper cervical spinal nerves. Each, however, runs into the skull cavity alongside of the spinal cord and, getting a few filaments from the medulla oblongata, passes out along with the glossopharyngeal and vagus nerves.

Outside the skull it divides into two branches, one of which joins the vagus trunk, while the other is distributed to muscles about the shoulder.

The *twelfth pair* of cranial nerves (*hypoglossals*), *XII*, arise from the sides of the medulla oblongata; they are distributed mainly to the muscles of the tongue and hyoid bone.

It must be remembered that the cranial nerves, like the spinal nerves, are really bundles containing hundreds of nerve fibers having various destinations. Just as in the spinal nerve plexuses bundles of fibers cross from over one nerve-trunk to another, so in many of the cranial nerves, especially the fifth and seventh, there are branchings from one nerve to another, making it difficult to tell in many cases from what part of the brain the nerves to a special part have come; for example, it was believed for a long time that the dendrons mediating the sense of taste enter the brain as part of the trigeminal nerve. It is now practically certain that they enter instead by way of the facial and glossopharyngeal.

White and Gray Matter. In preceding paragraphs the occurrence of white and gray matter in the central nervous system has been mentioned. In the paragraph on myelin sheaths (p. 146) the difference between them was described. It may be worth while, for emphasis, to state again this difference before discussing more specifically their distribution in the nervous system. White matter consists of medullated axons or dendrons, and is concerned functionally, therefore, with the conduction of impulses from point to point. Gray matter consists of cell-bodies, dendrites, and parts of axons, and in it and it alone are the synapses found over which impulses pass across from one neuron to another. Gray matter, therefore, is concerned with the distribution of nerve impulses among the neurons. In it also, as we shall see, take place the modifications which nerve impulses undergo during their passage through the central nervous system.

Most of the gray matter of the Body is found in three special regions. These are: (1) the gray columns of the spinal cord; (2) a layer about 2 mm. ($\frac{3}{32}$ in.) thick over the entire outer surface of the cerebral hemispheres, including the mesial surface of each, and (3) a similar layer over the surface of the cerebellum. In addition to these chief gray regions there are a number of small masses of gray matter distributed in various parts of the Body.

Some of these are imbedded in the brain; others are outside the central nervous system altogether. Those within the central nervous system are known as *nuclei*,* those outside it as ganglia.

The gray nuclei are found in the following regions: (1) The base of the cerebrum; these are known as the *basal nuclei* and include the *optic thalami*, the *caudate*, and the *lenticular* nuclei; (2) the base of the cerebellum; here are several pairs of nuclei, including the *dentate* nuclei; (3) the midbrain; here are several small nuclei, the *superior* and *inferior colliculi* (corpora quadrigemina), the *external* and *internal geniculate* bodies, and the *red nucleus;* (4) the medulla; all the gray matter of the medulla is contained within its nuclei. They constitute the so-called *deep-origins* of those cranial nerves which arise in the medulla.

All nerve-ganglia in the Body, using the term ganglia in the restricted sense suggested above, fall into two groups: (1) Those which contain the cell-bodies of sensory neurons; in this group belong all dorsal root-ganglia of spinal nerves (see p. 155), likewise the ganglia which are found on some of the cranial nerves; (2) the so-called *sympathetic* or autonomic ganglia which are described in the next paragraph.

The Sympathetic or Autonomic System. The ganglia which form the main centers of the sympathetic nervous system lie in two rows (s, Fig. 2), one on either side of the bodies of the vertebræ. Each ganglion is united by a nerve-trunk with the one in front of it, and so two great chains are formed reaching from the base of the skull to the coccyx. In the trunk region these chains lie in the ventral cavity. The ganglia on these chains are forty-nine in number, viz., twenty-four pairs, and a single one in front of the coccyx in which both chains terminate. They are named from the regions of the vertebral column near which they lie; there being three cervical, twelve thoracic, four lumbar, and five sacral pairs.

Each sympathetic ganglion is united by *communicating branches* with the neighboring spinal nerves, and near the skull with various cranial nerves also; while from the ganglia and their uniting cords arise numerous trunks, many of which, in the thoracic and abdominal cavities, form plexuses, from which in turn nerves are given

* It must be understood that the term nucleus as applied to a mass of gray nervous matter has an entirely different significance than when applied to a part of a single cell.

off to the viscera. These plexuses frequently possess numerous ganglia of their own; two of the most important are the *cardiac plexus* which lies on the dorsal side of the heart, and the *solar plexus* which lies in the abdominal cavity and supplies nerves to the stomach, liver, kidneys, and intestines. Many of the sympathetic nerves finally end in the walls of the blood vessels of various organs. To the naked eye they are commonly grayer in color than the cerebrospinal nerves. This is because their myelin sheaths are greatly reduced or absent.

CHAPTER X

GENERAL PHYSIOLOGY OF THE NERVOUS SYSTEM. REFLEXES

Conduction within Single Neurons. Since the nervous system, whose function as a whole is the conduction of impulses from sensory regions to motor ones, is made up of individual neurons, the study of its physiology can best be begun by considering the phenomenon of conduction as exhibited in single neurons, passing later to conduction as it involves more neurons than one.

The passage of an impulse along a nerve is attended by no visible alteration of the nerve itself; it is impossible to tell by looking at a nerve whether it is carrying impulses or not. For this reason nerve impulses can only be studied indirectly. If as the result of stimulating a motor nerve at some point along its course the muscle in which it terminates is thrown into contraction the obvious conclusion is that nerve impulses are passing from the point of stimulation to the muscle. When the prick of a finger gives rise within the brain to a conscious sensation of pain we know that a nerve impulse must have passed between the finger and the brain, although we would be unable to detect any sign of its passage if the nerve were visible throughout its length. In addition to these methods of studying nerve impulses, in which the passage of the impulse is made known through its effect on some other part of the Body, we have a method which depends upon the fact that activity of nerve, like activity of muscle or any other living tissue, is accompanied by changes of electrical potential which may give rise to action currents (p. 124). Every time an impulse passes along a nerve it is accompanied by this electrical alteration. Sensitive electrometers applied to nerves will indicate the passage of impulses under their points of contact.

By the use of these methods of studying nerve impulses we have learned many things about them, although much more remains unknown.

How Nerve Impulses Are Aroused. We know that nerve impulses may be started in various ways. A sharp blow on a living

nerve starts impulses traveling along it; a good example of this is the effect of striking the "funny" bone. Nerves may be stimulated by heat or by cold, by chemical agents or by an electric spark. Whatever the nature of the stimulus the nerve impulse which it arouses is, so far as we can tell, very much the same in all cases.

Speed of Nerve Impulses. The nerve impulse travels from the point of stimulation over the neuron at a regular and rather slow rate which probably varies somewhat in different animals and in different nerves of the same animal. In frogs' nerves at ordinary room temperatures the rate approximates 30 meters (97 ft.) per second. In human nerves at body temperature (98.5° F.) the rate is about four times as high.

Spread of Impulses in Both Directions. Through observations of the action currents of nerves it has been shown that the impulse spreads from the point of stimulation in both directions along the neuron, finally traversing all parts of it. This fact could never have been demonstrated if the existence of the action currents were unknown because our only other method of detecting the presence of nerve impulses depends upon the production of effects in the organs to which the neurons lead; and in the body each neuron has such connection only at one end; a nerve impulse imparted to a motor nerve will cause contraction in its connected muscle but produces no effect whatever at its other end.

Fatigue. It has been proven beyond question that the passage of impulses over nerve-fibers does not fatigue them except for a small fraction of a second; they recover almost instantaneously to precisely their state before the impulse passed. In this respect the nerve is comparable to a telephone wire; in each case the message is transmitted without impairing the ability of the structure to transmit other messages.

We learned in connection with our study of muscular fatigue (p. 119) to look upon fatigue as the result of the accumulation of sodium lactate or some similarly acting substance. Its absence from active nerve-fibers indicates one of two things. Either the transmission of nerve impulses does not involve the production of fatigue substances or the fiber is able to get rid of such as are produced so quickly that they cannot affect its working. Exceedingly delicate tests which have recently been devised indicate

that in nerve trunks there is a small production of carbon dioxid, greater during the passage of nerve impulses than when the nerve is resting. This gas is known to be a product of oxidation and its occurrence is taken to mean that chemical processes do go on in connection with nervous activity.

They must be of very small magnitude, however, for their products are so quickly dissipated as not to hinder the functioning of the nerve at all.

While indefatigability is thus seen to be a property of nerve fibres we shall learn presently that other nervous structures are highly susceptible to it. Nervous fatigue is a common phenomenon, but it is localized in the region of the synapses and not in the axons or dendrons.

Nature of the Nerve Impulse. Although we know these things about nerve impulses, we do not know what the nerve impulse itself really is. There have been many interesting and ingenious theories of its nature proposed. Perhaps the most satisfactory yet suggested starts with the general conception of stimulation as a process by which cell membranes are increased in permeability (p. 30). As applied to nerve cells this would mean that there is a protoplasmic membrane, perhaps surrounding each axon and separating it from the overlying myelin sheath (also inclosing individual dendrites), which becomes more permeable when any adequate stimulus is brought to bear: the increase in permeability allows some previously imprisoned molecules or ions to escape. This is looked upon as the first result of stimulation. The escape of molecules or ions upsets the equilibrium previously prevailing in the protoplasm of the axon, and there is necessarily a readjustment of the structures and forces present in the direction of a new equilibrium. This readjustment takes place very rapidly, occupying less than 0.002 second. A feature of the new equilibrium is that it has a lower electrical potential than prevails in the normal axon, thus enabling an "action current" to be demonstrated between unstimulated and stimulated areas of nerves. The difference of potential is sufficient to cause an actual movement of ions (or electrons) between the stimulated point and immediately adjacent inactive areas; the result is to upset the equilibrium in the latter; their potential falls in turn, and the areas next beyond become involved; thus the disturbance spreads along the axon. Mean-

while at each point where a shift to a new equilibrium has occurred processes are set in motion whose effect is to restore the former state. These restorative processes take slightly longer than the initial upsets (0.01 second as compared with 0.002 second); they appear to include oxidation as the means by which the energy necessary to the restoration is provided; when complete the nerve fiber is perfectly recovered, no residuum of fatigue remaining. According to this view the nerve impulse is thus a phase of disturbed equilibrium sweeping along the axon, followed immediately by a phase of recovery. The first phase is illustrated by a row of dominoes set on end, each upset by the fall of its neighbor; if we imagine an arrangement whereby each as it falls actuates a device that sets it up again we have an analogy to the second phase.

Obviously one stimulus cannot be effective if it follows so closely on the track of another as not to allow time for recovery. In other words, nervous conduction cannot be strictly continuous, but must necessarily be composed of separate brief impulses. Thus the name commonly applied to the nervous discharge is justified. During prolonged excitation of a nerve, as in sustained voluntary contraction of a muscle, the individual impulses follow each other in rapid succession (50–100 per second).

From the picture of the nerve impulse given above it follows that the *magnitude* of the impulse depends on the amount of shift resulting from the upset of equilibrium. This amount of shift is determined by the state of the nerve at the instant of stimulation; in other words, the nerve obeys the "all-or-nothing" principle (p. 105). Since it is safe to assume that the state of nerves in the Body tends to be about uniform we are forced to the conclusion that *individual* nerve impulses are on the whole of *nearly equal* intensity. This is important in view of the familiar fact that nervous activities in general may show widely different intensities. The prevailing explanation accounts for this on the ground that nervous activities depend, not on single impulses, but on *streams of impulses* which latter may vary even though the individual component impulses are nearly equal. In accordance with this view we have to suppose that a weak stimulus gives rise to one sort of stream of impulses, a stronger stimulus to a differet sort and so on.

Conduction Involving More Than One Neuron. Reflexes. In the actual passage of nerve impulses through the Body more neurons than one are always involved. Let us examine a simple case of conduction by which the Body adapts itself to its surroundings. Accidentally my finger comes in contact with a hot surface. Quite involuntarily I jerk my hand away. The chain of events is as follows: the skin of the hand is stimulated by the heat; the sensory neurons in the nerve supplying that part of the hand convey the nerve impulses thus aroused to the central nervous system; here the impulses are conveyed to the motor neurons leading to the muscle which retracts the arm; upon the arrival of the impulses within the muscle the latter is stimulated to contract. The whole process is entirely mechanical; none of the structures involved has any knowledge that the hand is in danger of being severely burnt, or that retraction of the arm will save it. It is an example of an adaptive mechanism. Such a chain of events as the one described constitutes a *simple reflex* and typifies the fundamental basis of all nervous activity within the organism. Our study of the operation of the nervous system will consist throughout of enlargements and modifications of this elementary conception of nervous activity as conduction of nerve impulses from receptor to active tissue. In its broadest sense any such act of conduction may be termed a reflex, and so we shall define the word. The neurons involved in the transmission of the impulse from receptor to muscle make up the *reflex arc*. The simplest imaginable reflex arc must include at least two neurons, the sensory neuron which brings the impulses from the receptor to the centre (these are known as *afferent* impulses; p. 179), and the motor neuron which conveys the impulses from the centre to the motor organ (*efferent* impulses). Undoubtedly most reflex arcs in the Body include, in addition, one or more internuncial or connecting neurons interposed between the sensory and motor neurons.

Anatomical Arrangement. The anatomical relationships of the various neurons which make up the reflex arc are indicated in figure 63. For simplicity the spinal cord is taken as the part of the central nervous system pictured. The receptor communicates with the cell-body of the sensory neuron by means of a dendron as previously described (p. 144). The cell-body of the sensory neuron always lies outside the central nervous system in a dorsal

root ganglion; its axon extends thence by way of the dorsal root of the spinal nerve into the spinal cord (or brain) and enters the dorsal column of white matter (p. 152).

Within the central nervous system is located the cell-body of the motor neuron which forms the outgoing part of the path. This will be found in the *ventral horn* of gray matter of the spinal cord. The simple reflex arc is formed by one of the branches of the sensory axon which penetrates the gray matter and whose end arborization makes synaptic connection with the dendrites of the motor neuron.

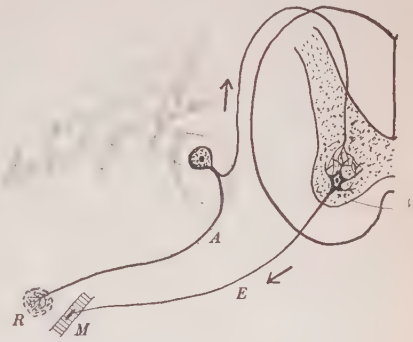


FIG. 63.—Diagram of the simple reflex arc. *R*, receptor; *A*, afferent (sensory) neuron; *E*, efferent (motor) neuron; *M*, muscle.

Reflex Arcs Not Rigidly Fixed Paths. Although a given sensory stimulus usually arouses the same sort of reflex response every time it is applied, this does not mean that the reflex path followed in such a case is the only one into which that sensory neuron leads. Very different reflex responses may originate in the same receptor. A good illustration of this is furnished by certain reflexes through the eye. If I see that a small floating particle threatens my eye I am apt to wink; if a flying insect approaches I am more likely to turn my head to one side; if the threatening object is a swiftly thrown baseball I will probably bring the hands before the face, or perhaps dodge to one side. All these actions are performed mechanically and are therefore true simple reflexes. The originating sensory impulses travel in each case over the same sensory neurons, those of the optic nerves. It is evident, then, that impulses coming in over the sensory neurons of the optic nerve do not have to pass over to any particular motor neuron, such as the one which leads to the muscle of winking, but may follow any one of various courses, finally terminating in muscles far distant from the eye. In fact, and this is one of the most important things to remember about the nervous system, there is such an extraordinary richness of connection among the various

neurons within the central nervous system that any sensory neuron may be brought into communication with any motor neuron.

This richness of connection is afforded anatomically through two rather simple arrangements. In the first place the axons of sensory neurons after entering the central nervous system continue along it for some distance, giving off branches, called *collaterals*, at various levels. In the spinal cord the dorsal white columns con-

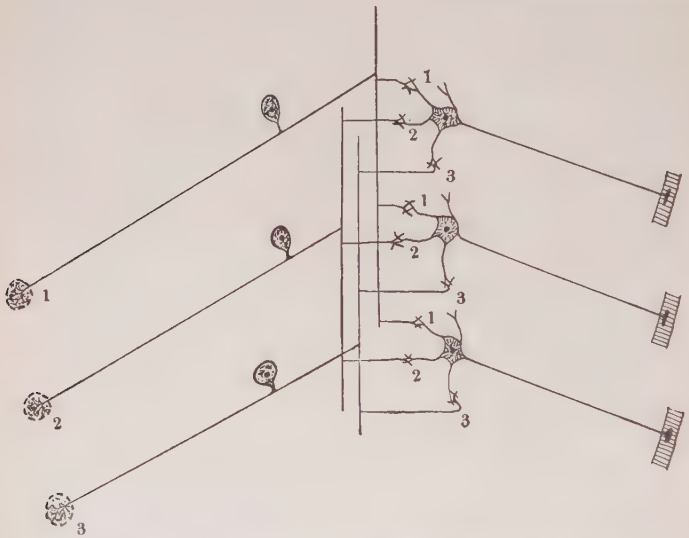


FIG. 64.—Diagram to illustrate how a single sensory neuron may communicate with several motor neurons, and a single motor neuron with several sensory neurons.

tain these axons. They extend toward the brain, but each gives off a branch which extends a short distance down the cord in the opposite direction. Each collateral terminates in an end arborization which communicates in turn with the dendrites of another neuron, either motor or internuncial. Thus each sensory neuron, besides its connection with one or more motor neurons, has connection with various internuncial neurons located in different parts of the central nervous system. The internuncial neurons likewise are richly branched, each branch terminating in a synaptic connection with another neuron, and this in turn may be an internuncial neuron, or may be a motor neuron. In the second

place the dendrites of all internuncial and motor neurons doubtless have synaptic connection with end arborizations of numerous neurons, sensory or internuncial as the case may be. Thus a sensory neuron has a wide choice of paths over which to send its impulses; and a motor neuron may receive impulses from a great variety of sources (Fig. 64).

Irreversible Conduction. In all this maze of connections and interconnections within the central nervous system, how is it that the impulses coming in at a sensory neuron always come out finally at a motor neuron instead of becoming switched sometimes to another sensory neuron? The orderly progress of impulses is insured by a very simple arrangement, namely, that impulses can pass freely across a synapse from end arborization to dendrites but can never pass in the reverse direction, from dendrites to end arborization. When a sensory neuron delivers its impulses to an internuncial neuron the impulses doubtless spread to all parts of the latter. They can leave it, however, only by way of its end arborizations, and these communicate only with the dendrites of motor neurons or of other internuncial neurons. The final outcome is bound to be a motor neuron since all internuncial neurons lead ultimately to them. Sensory neurons never receive impulses from other neurons because they have no dendrites within the central nervous system by which impulses might be received. (An apparent exception to this statement is seen in the nerves that supply some of the small blood vessels; see p. 395.) The portion of a sensory neuron which corresponds to the dendrites of a motor neuron is the dendron communicating with the receptor.

Graded Synaptic Resistance. Another question which naturally arises when one considers the innumerable courses which an impulse may take within the central nervous system is what determines the course it actually does take? Why, for instance, when my eye is threatened do I wink instead of opening my mouth, or why do I sometimes wink and sometimes dodge? A complete answer to this question cannot be made in the present state of our knowledge, but we have a fairly good general idea of the way in which nerve impulses are probably guided. A sensory neuron has several collaterals, each with its synaptic connection with another neuron. If we suppose these synapses

are not all alike, but that certain ones transmit the sort of stream of impulses generated by feeble stimuli more readily than do the others, such a stream spreading over the sensory neuron will pass most easily to that connecting neuron whose synapse offers least resistance to its passage. Thus we may imagine a stream of impulses spreading from neuron to neuron following always the path of least resistance until it finally terminates in a muscle which it arouses to activity. In the central nervous system the various paths of least resistance are so blocked out as to lead to adaptive motions; a prick on the finger causes retraction of the hurt hand; irritation in the nose causes the convulsive movements of the respiratory muscles which constitute a sneeze; in each case the motions are calculated to get rid of the source of irritation.

That adaptive reflexes are due to paths of least resistance blocked out from an infinite number of possible paths is strikingly illustrated by the effects of strychnine poisoning. This drug acts on the central nervous system in such a way as to abolish differences of synaptic resistance. When one suffering from the drug receives a stimulus by way of any sensory nerve the impulses, instead of following the usual path, spread over the whole central nervous system; all the muscles are stimulated simultaneously and the well-known strychnine convulsion results.

The Orderly Spreading of Reflexes. The conception of graded synaptic resistances explains also in a very satisfactory way the phenomenon of the orderly spreading of reflexes. A feeble stimulus produces reflex movement in those muscles only which are immediately concerned in the adaptive response; stronger stimuli involve more muscles, but only such as by their movement make the response more effective. For example, if a frog's hind leg is touched gently it will be drawn away from the source of irritation; a stronger stimulus is likely to cause contractions of such additional muscles as are required for jumping away from the point of danger. According to the "all-or-nothing" principle the individual impulses aroused by feeble stimuli are the same size as those aroused by strong. We can assume, however, either that the latter arouse more receptors, and so start more streams of impulses into being, or that the separate impulses aroused by strong stimuli are more effectively *timed* than those aroused by weak, and so can overcome enough additional resistance to enter

the paths leading to the jumping muscles; if we assume also that the paths to muscles not concerned in any way in the adaptive response have too high resistance to be passed at all, we can account for reflex actions of very great complexity.

Inherent and Acquired Reflexes. Certain reflexes occur from birth; the first time the child's lips are placed at the breast the reflex of sucking takes place; there will be withdrawal of an irritated limb from the source of irritation, and usually crying as well, from the very beginning; a new-born infant sneezes efficiently the very first time its nasal passages are irritated. Moreover, and this is important, the infant cannot help doing these things. The impulses move over paths that are blocked out as the nervous system develops. Although, as we shall learn, we have a certain degree of voluntary control over some of our inherent reflexes, their essentially automatic character should be emphasized. To contrast reflexes of this group with those of another group about to be described the distinguished Russian physiologist, Pavlov (pronounced Pavloff), designated them as *unconditioned* reflexes; signifying by the name that they are inherent, and therefore not conditioned on any process of learning.

In addition to the unconditioned reflexes with which he is born every individual acquires beginning not very long after birth, another set of reflexes, known as *conditioned* reflexes. The significant thing about these is that they may or may not be particularly useful to the organism; they exist because by some means paths of least resistance come into being between particular receptors and definite active tissues. They can be established at any time during life. Many, perhaps most, of them are developed volitionally; that is, we deliberately do a certain thing in response to a particular sensory stimulation so often that presently the response becomes automatic. Learning to drive a car is a good example of this. No better illustration of a non-useful conditioned reflex can be cited than the original one used by Pavlov in his researches on the subject. He started with the familiar unconditioned reflex found in most higher animals of "watering at the mouth" at the presence of food. In this reflex the organ of smell (or of taste) is the receptor, the reflex arc extends thence to the brain, and from the brain to the salivary glands, which are the active tissues concerned. In Pavlov's experiments a dog was

allowed to take food and at the same moment a particular note was struck on a piano; this was repeated frequently, and presently it was found that the reflex could be elicited by simply striking the note, without bringing any food into the situation at all.

Prior to the recognition of the existence and ease of development of conditioned reflexes much of the behavior of men and animals was difficult to interpret biologically; how an organism could come into possession of reflexes that might be of no biological advantage to it, or even in extreme cases distinctly harmful, was hard to explain in accordance with such firmly established generalizations as the "struggle for existence" and the "survival of the fittest." When we realize, however, that the nervous system is essentially plastic, that reflex paths may be laid down on what seems slight provocation, we can account for behavior otherwise difficult to understand.

It is both interesting and significant that as we go up the animal scale along one line of development, *i. e.*, that culminating in the highest insects, ants and bees, we find the whole nervous organization based on complex and highly co-ordinated, but completely automatic, and therefore unconditioned, reflexes, which we designate as instincts. Along the line of development culminating in man, on the other hand, the higher we look the less is behavior dominated by the unconditioned reflexes, and the more prominent in nervous organization are conditioned reflexes and volitional action.

Simple and Complex Reflexes. We have pictured reflexes more or less as though they arise from the stimulation of a single receptor and find expression in the activity of a single tissue. Many reflexes are, of course, of precisely this character; but in the daily life of almost any animal it happens frequently that several receptors are stimulated simultaneously, and the adaptive response is one that requires the interaction of a number of muscles. The spinal cord has considerable power of transforming impulse streams from more than one receptor into appropriate efferent (outgoing) streams, arousing several muscles to co-ordinated activity; but much less than is required for executing the most complicated reflex actions of which the Body is capable. Spinal-cord reflexes range from simple withdrawal of a limb from a source of irritation to acts as complex as the evacuation of the

bowels; the latter reflex involves the orderly interaction of a large number of muscles; it has been known, however, to occur normally in persons who have suffered complete severance of connection between spinal cord and brain, and is undoubtedly, therefore, a true spinal-cord reflex. Although complicated it falls considerably short of the complexity of such an act as walking, or even the maintenance of the upright posture in man. These latter actions, and many others ranking with them, are mediated through the brain, and our attention must now be turned to that organ.

Relation of the Brain to the Head Senses. The brain apparently owes its large size primarily to the fact that it constitutes the "central station" for three pairs of complex and highly developed sense organs, those of smell, hearing, and sight, as well as for the somewhat less complex organ of taste. As we shall learn when we come to study them directly, these organs communicate with the central nervous system by very large numbers of nerve paths; their complexity is such that they can function only through this great richness of central connection. To provide all the synaptic junctions necessary to enable them to play their part in mediating the many reflexes of which they are capable requires the presence of enormous numbers of internuncial neurons; moreover, the head region has its quota of receptors similar to those found in the Body at large, receptors for touch, pain, warmth and cold, and muscle sense, all of which have abundant central connections; thus the disproportionate size of that part of the central nervous system which lies at the front end of the body can be accounted for. A little reflection will show, furthermore, that these senses, especially sight and hearing, contribute to the sensory basis of the great majority of complicated reflexes. We need not be surprised, then, to discover that the brain has much greater power to organize streams of afferent impulses from various sources into co-ordinated streams of efferent impulses than the spinal cord has.

Special Significance of the Distance Receptors. Three of the head senses listed above, smell, hearing, and sight, occupy a position of particular importance in the whole machinery of adjustment in that they give information of what is happening at a distance. The advantage of this is that bodily movements may be less hurried, and still be serviceable. It is clear that information

which reaches us only as the object which gives rise to it strikes the Body must evoke an immediate response if the latter is to be useful. This is generally the case with information received through the so-called contact senses (p. 222); reflexes aroused through them take no more time than is required for the passage of impulses over the nerve paths involved, plus a delay of a brief fraction of a second at each synapse crossed; in most reflexes of this class the total time between stimulus and response is in the neighborhood of 0.06–0.1 second. Many reflexes evoked by stimulation of distance receptors are, of course, equally prompt; when a horse pricks up its ears at a sound there is no delay in the action. But it is clear that in many cases the interests of the organism might be better served by a delayed response than by one that follows instantly on the stimulation. Immediate responses are of necessity essentially automatic; the nerve path followed by the impulses must be blocked out before the receptors are stimulated, as there is no time to make readjustments after stimulation begins. Given a means of delaying the response and a stimulation that gives information of distant happenings it is no longer necessary that the action be so automatic; it becomes possible for selection to be made among several possible reflexes, and for the one that promises to be most useful to be carried out; in other words, the element of choice enters as a factor in reflex action.

The Cerebrum Provides Machinery for Choice. It is clear that in order for choice among various responses to be possible there must be some nervous mechanism for guiding the impulse stream pouring in from the region of stimulation to some selected outgoing path. Furthermore, there must be some basis for choice other than mere chance, since only thus can the organism derive any biological advantage from the power of choice. The machinery resides in that subdivision of the brain known as the *cerebrum* (p. 153); the basis of choice can depend on only one thing, namely, previous experience. The cerebrum is, then, an organ which modifies certain reflexes in accordance with past experience. In the next chapter we shall study it in this light. Incidentally it may be noted that associated with and growing out of this primary function is the whole gamut of higher mental and emotional functions which make up what we know as the mind.

CHAPTER XI

STRUCTURE, NERVE CONNECTIONS, AND FUNCTIONS OF THE CEREBRUM

The Cerebrum in Relation to Bodily Activity. In the preceding chapter two classes of reflexes, *inherent*, or unconditioned, and *acquired*, or conditioned, have been described. A fact it is important we should grasp, is that a large part of all the activities of all animals belong to the former of these classes. Indeed as we go down the scale and examine such animals as fish, frogs, and turtles, it is a matter of some difficulty to prove that any of their acts involve higher nervous manifestations. In man and the higher animals, however, we recognize many activities which are obviously not automatic, as the inherent reflexes are, and some that do not appear to be of a reflex nature at all. The latter include all acts which we describe as *volitional*. For the performance of these the *cerebrum* is essential. We will get an idea of the significance of the cerebrum in relation to bodily activity, by noting the way in which it may modify such activity.

A Normal Animal Compared with a "Reflex" One. Let us imagine that we have side by side before us two living animals of the same species, one normal in every respect, the other in the "reflex" condition; that is, having had the cerebrum destroyed but the remainder of the nervous system uninjured. Disregarding for the present the phenomenon of consciousness and looking at both animals simply as pieces of machinery three striking differences between them are manifest: 1. The "reflex" animal always responds to adequate stimulation by a predictable response; the intact animal sometimes responds and sometimes does not. 2. The "reflex" animal does not move except when stimulated, while the intact animal often moves without any apparent reason. 3. The amount of response given by the "reflex" animal bears some relation to the intensity of the exciting stimulus, whereas in the normal animal an apparently feeble stimulus may arouse a vigorous and long-continued response. An example of this last is the running of a dog to its master upon hearing his

whistle. The stimulus may be a very faint one, the motions which it arouses are exceedingly vigorous and complicated.

All these differences depend at bottom upon a single fundamental difference between the two animals which is this: in the "reflex" animal the *immediate stimulus* dominates the situation completely; in the intact animal the immediate stimulus is only one factor of many which together determine what the response shall be. The superior practical efficiency of the intact animal as an adaptive organism depends upon this power, resident in the cerebrum, of modifying immediate stimuli in accordance with the demands of less obvious considerations. To illustrate: a hungry man perceiving food would inevitably respond to the double stimulus of hunger and the sight of food by taking the food and eating it if he acted on a purely reflex basis; his actual response to these stimuli will depend, however, upon whether they are in harmony with or opposed to certain more remote factors, such as the question whether the food is of a sort that will agree with him, or whether he is likely to need it more urgently at some future time than at present.

Before entering upon a fuller discussion of the functions of the cerebrum, its structure and its connections with lower nerve-centres must be described.

The Cerebrum Dependent on the Receptor System. If the cerebrum is to introduce remote considerations as factors in determining the nature of reflex responses it must have within it the knowledge upon which these remote considerations are based. That the cerebrum has little original endowment of knowledge is evident from study of infants, who during the first months are perfect examples of "reflex" organisms. The equipment which the cerebrum finally obtains must be got bit by bit by experience or the teaching of others. Since the receptor system is the organism's only means of acquiring information, the cerebrum must be in communication with this system if it is to learn anything whatsoever.

Afferent Paths of the Cerebrum. We have learned in previous paragraphs that all sensory neurons lead directly into the central nervous system and there have numerous synaptic connections with internuncial neurons. These connections are all, however, with the possible exception of those of the sense of smell, made

in gray matter of the spinal cord, the medulla, or the midbrain. In order for impulses coming in over these sensory neurons to reach the cerebrum there must be communication by internuncial neurons between the terminations of the sensory neurons and the cerebrum. As a matter of fact such connections are richly supplied. Some of the most conspicuous tracts of white matter in the central nervous system consist of the myelinated axons of internuncial neurons which form connecting links between sensory neurons and the cerebrum. Since the cerebrum is the crown of the entire nervous system it is used as a landmark in describing other nervous structures. Thus nerve paths which convey impulses toward the cerebrum are called *afferent* paths; those carrying impulses away from it are *efferent* paths. According to this classification all sensory neurons are afferent and all motor ones efferent, while internuncial neurons are either afferent or efferent according as they carry impulses toward the cerebrum or away from it.

Tracing Nerve Paths. Wallerian Degeneration. One of the very satisfactory achievements of biologists has been the resolution of the apparently inextricable tangle of gray and white matter of the central nervous system into a system of fairly definite nerve tracts whose origins, courses, and terminations are known. Our present knowledge is the result of various methods of study. Perhaps the most fruitful has rested upon recognition of three facts: first, that white matter always consists of myelinated axons or dendrons; second, that axons and dendrons are always outgrowths of cell-bodies which are to be looked for in gray matter; and third, the fact discovered by the English physiologist, Waller, in 1852, that axons or dendrons cut off from connection with their cell-bodies undergo degeneration in a few days. Because of this latter fact if a cut be made anywhere in the central nervous system of an animal, and the animal be killed a few days later and its spinal cord and brain examined microscopically, the direction and extent of degeneration reveal the relation of the severed fibers to the rest of the nervous system. If the degeneration is all toward the head the severed tract must be an afferent one with cell-bodies somewhere below the cut. Backward degeneration would signify an efferent tract with its origin somewhere forward of the point of injury. Wallerian degeneration is not difficult to

follow because it is fatty and the drops of fat in the degenerated region can be plainly revealed by the application of osmic acid, which turns them black.

Successive Myelination. Another valuable method of tracing nerve tracts was discovered by Flechsig, who found that during the embryonic development of the animal the axons of individual tracts all become myelinated together, while different tracts receive their myelin sheaths at different periods of development.

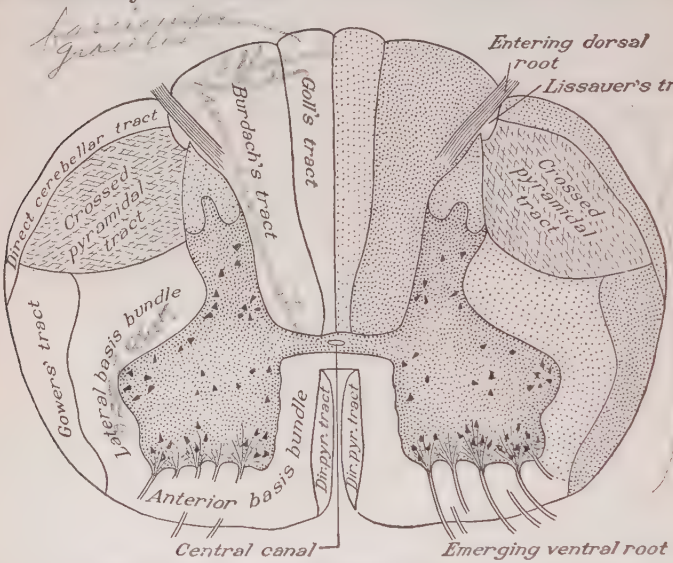


FIG. 65.—Diagrammatic transverse section of the spinal cord showing the conduction paths. (Cunningham.)

Thus by examining a large series of embryos in all stages the various tracts can be picked out.

Paths of the Various Senses. For convenience in describing the paths by which information is conveyed from the various receptors to the cerebrum, the receptors will be classified as body sense receptors and head sense receptors. The group of body senses includes all those senses such as touch, pain, muscle sense, etc., whose receptors are for the most part in parts of the Body other than the head, and which therefore communicate with the central nervous system by way of spinal nerves. The head senses, sight, hearing, taste, and smell, are those from which stimuli are car-

ried over cranial nerves to the medulla or midbrain, or in the case of the sense of smell directly into the cerebrum.

Tracts of Body Sense. Sensory neurons of body sense enter the spinal cord all along its length. Afferent paths within the cord begin, therefore, at its extreme end. These are to be looked for, as previously stated, in the columns of white matter which make up the greater part of the substance of the cord. Two distinct regions of white matter in each half of the cord have been

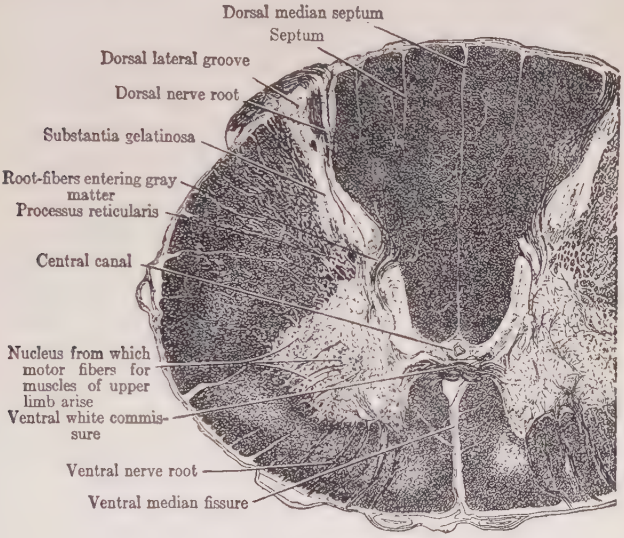


FIG. 66.—Cross-section through the human spinal cord at the level of the fifth cervical nerve, stained by a method which leaves the gray matter uncolored, but colors the white matter dark. (From Cunningham's Anatomy.)

shown to consist chiefly of afferent neurons leading toward the cerebrum. These are: first, the dorsal columns, each of which consists of two rather well-marked bundles of axons, the so-called *fasciculus gracilis* (*Column of Goll*) next the dorsal fissure, and the *fasciculus cuneatus* (*Column of Burdach*) next to the dorsal horn of gray matter; second, the ventrolateral tracts which lie next to the ventral horns of gray matter, surrounding them on the sides and below (Fig. 65). It is thought that the dorsal columns consist chiefly if not wholly of the axons of sensory neurons which, entering the cord by the dorsal roots of spinal nerves, extend forward within the dorsal columns, giving off collaterals into the

gray matter at various levels. Only a part of the sensory axons which enter the dorsal columns continue along them as far as the medulla; the others after extending a short distance plunge into the gray matter and terminate in synaptic connection with internuncial neurons. The ventrolateral afferent columns consist chiefly of internuncial neurons which communicate, presumably, with those sensory neurons which do not themselves extend all the way to the medulla; these columns serve, therefore, to afford cerebral communication to those sensory neurons which terminate within the gray matter of the cord.

None of the afferent axons coming up the cord by the tracts just described extend further than the medulla; they all terminate there in masses of gray matter known as the *gracile* and *cuneate nuclei;* here they form synaptic connections with a new set of internuncial neurons which continue the path toward the cerebrum. These tracts, which from their ribbon-like appearance have been named the *fillets,* cross the mid-line at a point in the medulla known as the *sensory decussation;* so that sensory stimuli from the right half of the Body are carried to the left cerebral hemisphere, and those from the left half of the Body to the right hemisphere. Forward of the sensory decussation the fillets continue as a tract known as the *lemniscus;* this extends to the optic thalami, whence new neurons continue the path to the final destination in the cortex of the cerebrum (see page 181).

In the lateral margins of the spinal cord are tracts known as the *direct cerebellar* tract and *Gower's* tract (Fig. 65), which consist of the axons of internuncial neurons that pass up to the brain stem and directly through it by way of the peduncles to the cerebellum. The cell-bodies of these axons are in the gray matter of the cord and have synaptic connection with branches of sensory neurons, particularly neurons of muscle sense. These tracts are believed to constitute the chief channels by which muscle sense exerts its influence on the cerebellum. (See p. 202.)

Tracts of the Head Senses. The senses of sight and hearing are the head senses whose central connections are best known. The central connections of the sense of smell are imperfectly known; those of taste practically not at all. Axons conveying *visual impulses* enter the midbrain by way of the optic nerves and optic tracts and terminate for the most part in nuclei of the

midbrain, the external geniculates and superior colliculi; some of them appear to terminate in basal nuclei of the cerebrum, the optic thalami. In all these nuclei synaptic connection is made with new neurons which carry the impulses into the cerebrum.

Auditory impulses enter the medulla by way of the acoustic nerves. The axons of the nerves themselves terminate in nuclei of the medulla, the *auditory nuclei;* new neurons continue the path thence across the mid-line of the medulla and forward into the midbrain terminating in the internal geniculate nuclei and the inferior colliculi. From these nuclei a third set of neurons continue the path to the cerebrum.

General Structure of the Cerebrum. This organ consists, as previously stated, of an outer surface of gray matter, two millimeters thick, overlying a mass of white matter; the whole held together by neuroglia and connective tissue, and mounted upon the midbrain as upon a stalk. Because of the convoluted surface of the cerebrum the total amount of superficial gray matter is much greater than it would be if the cerebrum were smooth. This layer of gray matter is the region wherein occur those special activities which set the cerebrum above the rest of the nervous system. It is called the *cortex cerebri,* or for convenience simply the *cortex.*

Structure of the Cortex. The cortex cerebri consists for the most part of neurons with small cell-bodies having much branched processes, signifying rich synaptic connections. Many of these neurons appear to be confined altogether within the cortex; others give off myelinated axons into the underlying white matter. Interspersed with these small cell-bodies are others which are much larger, which are pyramidal in shape, and which always give off a large axon into the white matter. From their shape and size these are known as large pyramidal cells. In a certain region of the cortex, known as the motor area, the pyramidal cells are relatively gigantic, being just at the limit of naked-eye visibility.

The White Matter of the Cerebrum. This consists of myelinated axons classified according to their course and distribution into three groups. The so-called *projection fibers* (Fig. 67) are the axons by which the cortex is brought into connection with the other parts of the nervous system. These include *afferent* projection fibers, which are the continuations within the cerebrum of the

various sensory paths described in previous paragraphs (see p. 180), and *efferent* projection fibers, which convey impulses from the cortex to the rest of the Body.

At the base of the cerebrum, where it rests upon the midbrain, all the projection fibers, both afferent and efferent, are crowded together into a restricted space between two of the basal nuclei. This region is known as the *internal capsule*. As the fibers emerge

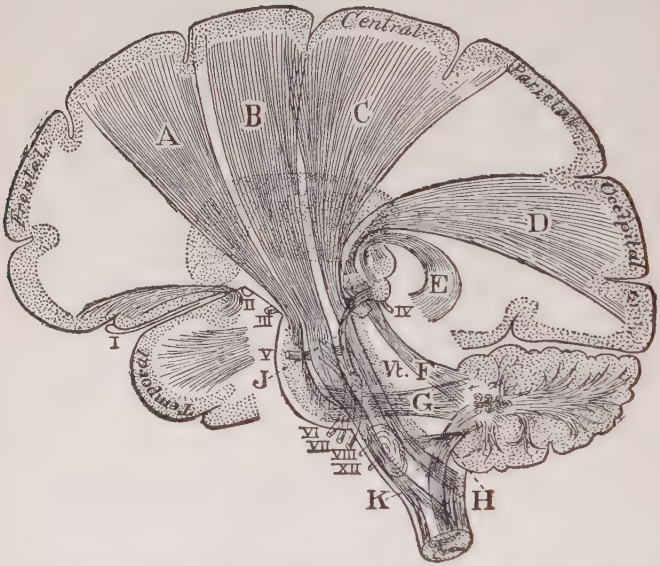


FIG. 67.—Diagram of the projection fibers of the cerebrum (from Starr). *B*, motor (pyramidal) tract; *C*, body-sense tract; *D*, visual tract; *E*, auditory tract; *F*, *G* and *H*, upper, middle and lower peduncles of cerebellum; *K*, decussation of pyramids. Numerals refer to cranial nerves.

thence into the roomy cerebrum they spread apart on their way to the different parts of the cortex forming the *corona radiata*.

The second group of cerebral axons are the *association fibers*. These pass between one part of the cortex and another within the same hemisphere, enabling impulses to travel freely among the cortical cells. The third group of cerebral axons are the *commissural* fibers which pass between cortical areas in opposite hemispheres; these serve to unify the anatomically double cerebrum into a single physiological organ; the *corpus callosum* (*Cc*, Fig. 60) is made up of commissural fibers.

Lobes of the Cerebrum. The convolutions of the cerebrum are sufficiently constant in number and position to serve as landmarks in locating particular regions. The individual *convolutions*, or *gyri*, have been given specific names, as have also the *fissures*, or *sulci*, which separate them. For our purposes it is necessary to mention by name only those fissures which mark off the grand divisions, or *lobes*, of the cerebrum. The division of the cerebrum into lobes is purely arbitrary, and is made for greater ease in describing it. In general the lobes correspond in position to the overlying skull bones for which they are named. The sulci which mark the boundaries of the lobes are indicated in Fig. 59. They are the *lateral sulcus* (fissure of *Sylvius*), the *central sulcus* (fissure of *Rolando*), and the *parieto-occipital* fissure (visible from the exterior only as the *preoccipital notch*). The *frontal* lobe is that part of the cerebrum above the lateral sulcus and in front of the central; the *parietal* lobe is between the central and parieto-occipital sulci; the *occipital* lobe is the wedge-shaped portion behind the parieto-occipital fissure; the *temporal* lobe is below the lateral sulcus; it is the only one of the lobes which is sharply set off as a distinct region.

Cortical Localization. A problem of much interest in connection with the study of cerebral functions is whether there is division of labor among the various parts of the cortex. Do certain groups of cells perform certain special functions, or are all cortical activities shared in by all the cells? This is not the place for a history of the solution of this problem. Suffice it to say that we now have positive proof of a high degree of specialization of function in the cortex.

Sensory Areas. In previous paragraphs (p. 180) the paths of the various senses were traced as far as their entrance into the cerebrum by way of the internal capsule. We must now continue the paths to their cortical terminations. The body sense fibers pass to that part of the parietal lobe just behind the central sulcus; the region where they terminate is the *body sense area*. The visual tracts end in the occipital lobes in the *visual areas*. The auditory tracts terminate in the temporal lobes in a region just below and within the lateral sulcus; this region constitutes the *auditory area*. Although the paths of smell and taste are imperfectly known, their cortical terminations have been fairly well established. The

olfactory area is supposed to be in the temporal lobe (hippocampal gyrus). The area for taste, *gustatory area,* is thought to be also in the temporal lobe, probably adjacent to the area for smell. Since the nerve-paths of the various senses lead directly to these areas, and since destruction of any one of them, by accident or disease, results in loss of the particular sense whose area is involved, we must conclude that the sensory areas are the receiving stations of the cerebrum. All afferent projection fibers entering the cerebrum terminate in one or another of the sensory areas. Within these areas they have synaptic connection with the association neurons of the region.

The Motor Area and the Pyramidal Tracts. In each hemisphere a region of the frontal lobe just in front of the central sulcus contains numerous giant pyramidal cells whose axons extend into the white matter and are grouped together in the internal capsule as a conspicuous nerve tract, called the *pyramidal tract.* It extends through the midbrain to the medulla and appears upon the ventral surface of the latter as a well-marked anatomical feature. About midway of the medulla the pyramidal tracts cross the mid-line in the *decussation of the pyramids* (*K*, Fig. 67). This decussation is not complete; part of the fibers of each pyramidal tract continue along the same side of the medulla to the spinal cord and down the latter in the ventral column, forming the *direct pyramidal tract.* That part of each pyramidal tract which crosses over at the "decussation" proceeds along the spinal cord in the lateral column as the *crossed pyramidal tract* (Fig. 65). It appears that most of the fibers of the direct pyramidal tracts cross the mid-line in the spinal cord before reaching their terminations; so that the pyramidal tracts are finally crossed tracts. All the pyramidal axons have synaptic connection with the cells of motor neurons in the ventral horns of gray matter of the cord.

The pyramidal axons are branched at their tips, so that each communicates with several motor neurons. On p. 144 we saw that each motor neuron connects with a number of muscle-fibers. It follows that a considerable group of muscle-fibers is under the control of each pyramidal axon. When we recall the large numbers of fibers which go to make up even our smallest muscles, we see that this arrangement, which cuts down the number of nervous

elements required to operate the muscular system, does not at all impair the delicacy and efficiency of our muscular movements.

Since the pyramidal axons arise from cell-bodies within the cortex it is evident that the pyramidal tracts must be efferent paths. The intimate way in which the pyramidal fibers connect with the cell-bodies of motor neurons indicates that they form the paths by which the cerebrum exercises control over bodily movements. The anatomical evidence for that view has been corroborated and strengthened by physiological evidence. The German physiologists, Fritsch and Hitzig, showed that in dogs electrical excitation of those areas of the brain from which spring the pyramidal tracts is followed by movements of the muscles of the Body. They showed also that these are the only areas from which such movements can be elicited.

Upon the basis of all this evidence we are justified in looking upon the regions immediately in front of the central sulci as *motor areas*. These areas have been much studied physiologically in recent years. The brains of the higher apes have been preferred in these studies to those of lower animals because of their greater similarity to the human brain.

There have been a few observations upon the brains of human beings in cases where the surgical treatment of certain diseases has involved removal of portions of the skull overlying the central areas.

These recent studies have shown that there is a considerable localization within the motor areas themselves; stimulation of one point causes movements of the hand, of another the foot, of still another the head. They have shown incidentally, also, that the cerebral cortex is not painfully sensitive to direct stimulation. The men whose brains were excited electrically in the observations cited above were conscious throughout the procedure and reported no sensations of pain or discomfort at any stage.

Cortical "Reflex" Paths. The various sensory areas with their afferent nerve-paths afford means whereby impulses may enter the cerebrum from the different receptors; the motor areas, one in each hemisphere, with their efferent paths, provide for the passage of impulses from the cerebrum to the motor organs of the Body; the abundant equipment of association fibers within the cerebrum makes possible the passage of impulses across from sensory

areas to motor areas. We can picture, then, "reflex" arcs involving the cerebrum. Such arcs are necessarily complex, involving many more neurons than do the simple spinal cord reflex arcs already described. In a previous paragraph (p. 169) we saw that the simplest reflex arc through the cord involves at least two neurons, one sensory, and one motor. If we trace an arc involving the cortex from a receptor in the skin of the right hand, for example, to a retractor muscle of the right arm, we find in it at least six neurons and possibly many more. The six which are necessarily included are: 1, the sensory neuron which we suppose extends all the way from the receptor into the cord and up the dorsal column to a termination in the cuneate or gracile nucleus; 2, a neuron of the fillet tract, having its cell-body in the cuneate or gracile nucleus, and its axon extending through the medulla and midbrain and the white matter of the cerebrum, crossing the midline in the "sensory decussation" of the fillet, and terminating in the optic thalamus; 3, a neuron having its cell-body in the optic thalamus and its axon extending thence to make synaptic connection with a neuron of the body sense area in the left cerebral hemisphere; 4, the neuron just mentioned, having its cell-body in the body sense area and an axon which passes by way of the cerebral white matter to the motor area; 5, a pyramidal neuron of the motor area whose dendrites receive the impulse from the body sense neuron (4), and whose axon forms part of the pyramidal tract, crossing back to the right side of the Body in the decussation of the pyramids, and terminating in synaptic connection with the cell-body of a motor neuron in the ventral horn of gray matter of the cord; 6, the motor neuron which forms the last link in the chain, conveying the impulse from the pyramidal neuron to the muscle. It is doubtful whether any cortical arcs are actually composed of as few neurons as six; probably the simplest contain several additional association neurons within the cerebrum.

Cortical Responses Compared with Simple Reflexes. As an example of a simple reflex was cited the involuntary withdrawal of the hand from accidental contact with a hot body. It is easy to picture a situation in which the muscular action is precisely similar, but the nervous action involves the cortex of the cerebrum. Suppose, for example, my finger rests upon the terminals of an apparatus for generating electric shocks; I am told that when I

feel the shock I must withdraw my hand. The shock may be so feeble as to be barely perceptible. Under such circumstances the withdrawal must be voluntary and the response, therefore, must involve the cerebrum. The chief *objective* difference between voluntary withdrawal of the hand in response to feeble stimulation, and its involuntary retraction in response to strongly painful stimulation is that the former reaction requires a noticeably longer time than does the latter. The only simple reflex whose time has been satisfactorily measured in man is the winking reflex; this requires about 0.06 second for its completion. The quickest cortical actions take about 0.15 second. This difference in time is much greater than can be accounted for by supposing the cortical "reflex" to involve a greater length of nerve-fibers, and therefore must be due to the fact that it involves a greater number of neurons and consequently more synapses to be crossed.

An additional difference which we recognize *subjectively* between spinal reflexes and cortical responses is that while the former are involuntary and unconscious, the latter are voluntary responses to stimuli consciously perceived. This difference will be discussed more fully in a later paragraph, when the meaning of the terms "voluntary" and "consciously" shall have been considered.

Memory. We have seen that the primary function of the cerebrum is to introduce remote considerations as determining factors in the responses of the organisms. We have seen also that in order to do this the cerebrum must have an equipment of knowledge, which can be gained only through the receptor channels of the Body. The information which reaches the brain, to be of service, must be retained there until needed, and must be held in such a way as to be available when required.

The neurons of the nervous system generally act, in the main, as conductors pure and simple. When they are stimulated nerve impulses are aroused; these spread over them and escape by those synapses whose resistance is not too high; thus other neurons are involved and so the impulses advance to a motor termination.

The cortical neurons of the cerebrum owe their dominant position in the nervous system chiefly to a peculiar ability which they possess of "holding up" impulses which come to them, retaining them indefinitely, and giving them out again in the future, if necessary, over and over. This storing of impulses constitutes

memory. The "decerebrate" animal, because he is deprived of this property, must always respond immediately to adequate stimulation; the intact animal may respond immediately or may retain the stimulus as a memory to modify his future activities. Since the intact animal has within his cerebrum a store of impulses "held in leash," he may at any time become active through the liberation of some of them, without immediate external stimulation.

Association Areas. The different sensory areas and the motor areas occupy only a small part of the whole cerebral cortex. Most of the frontal lobes and large areas of the parietal and temporal lobes are not involved in the immediate reception of impulses, nor in their transmission to the Body. These areas are as richly supplied with interconnecting neurons as any part of the cortex. They are assumed, without very positive proof, to be the seat of a function we know the cerebrum to possess, that of *association*.

The Nature and Mechanism of Association. At birth the brain of the infant may be compared to a clean page. It bears no impressions of any sort. Such activities as the infant shows are purely reflex. In course of time sense impressions begin to come into the sensory areas of the cortex. These register themselves more or less definitely as memories, and presently the child is in possession of a considerable store of memories of various sorts. He may know the sound of his mother's voice or may recognize her face. As yet, however, there is no connection between these independent impressions. When in the child's mind that voice is associated with that face, so that he knows them as parts of a single whole, he has performed an act of *association*. From this time throughout his life his memory is not alone of the simple sound of the voice or the appearance of the face but of the mother whom he has learned to know by these associated impressions.

Acts of association are supposed to be carried on within the association areas of the cortex. We may picture the process in the example cited above somewhat as follows: The impression of the voice is held in the auditory area; that of the appearance of the face in the visual area; both these sensory areas have rich communications with neurons of the association areas. By some means impulses from the regions where these impressions are held meet in a particular group of cells of an association area. That

cell-group builds from these single related sense impressions, a composite, which is thereafter held in turn as a memory. As additional related information is gained the composite, or *concept*, is enlarged.

The union of related impressions into concepts does not necessarily involve loss or impairment of the fundamental impressions themselves; the child in whose mind is a definite concept of his mother retains also clear memories of her voice and her face. The paths of communication between the cells where are held the primary sense impressions and those where the resulting concepts are formed seem to remain always very easy of passage. The sound of the mother's voice calls up the entire concept of the mother with great clearness, even though years may have elapsed since it was heard.

Since concepts are held as memories they may serve in their turn as bases for more complex associations; these again by becoming memories may contribute to the associative process, and so the complex structure of the mind is built up, resting at bottom always upon primary sense impressions.

The act of association is essentially one of combining related memories; the formed associations become memories in their turn. For these reasons the term *associative memory* is used as more truly describing the nature of associative processes than the older expression "the association of ideas."

The use of a memory in forming one association does not interfere with its use in the formation of others. This ability of the cerebrum to use memories over and over again is a very valuable property since it enables us to make the utmost of all our knowledge.

Development of the Cortex. The increase in intellectual power which accompanies the growth of the child is not the result of any increase in the number of nerve-cells, for the child is born with his full number. It is, however, based upon their continuous development; this development consisting chiefly of greater and greater branching with correspondingly richer synaptic connections. At birth scarcely any cortical cells are sufficiently developed to be functional. The sensory areas first become so. The association areas reach their highest point of development at about the thirty-fifth year. At this age the anatomical progress of the brain comes to an end; all possible paths of association have been laid down.

This does not mean, however, that all possible associations have been formed. These continue to be formed so long as the brain continues active. It is probably true, however, that with advancing years there is a diminution in the freedom of associative activity; the brain no longer accomplishes daring feats of thought, such as constitute creative genius, but plods along in the ruts established by its earlier activities. This fact explains why conservative tendencies usually become more pronounced as age advances.

The Functions of Associative Memory. It is because the cerebrum is able to form associative memories that the organism can adjust its responses with due regard to remote as well as to immediate considerations. Incoming stimuli, which in a "reflex" animal would produce a definite response of a certain kind, are in an intact animal balanced against such related associative memories as the animal possesses; if these indicate that the natural reflex response is the proper one to make, the animal responds as does the "reflex" one; if, however, they indicate a different line of action as more advantageous, the animal substitutes for the natural reflex response a different one, suited to the situation.

Associative memory also forms the basis for the execution of complex movements from feeble, immediate stimuli, or in their absence; the young puppy responds to his master's whistle only by a pricking of the ears; in the older dog the sound of the whistle arouses a chain of associative memories and under their impelling force he executes the complex movements which carry him to his master's feet.

In order that associative memory may influence bodily activities it must have access to the efferent nerve-paths of the cerebrum. This access it has through rich connections from the association areas to the motor areas. It must have also the power to stimulate the efferent nerves. This power it exercises through the function of *volition*.

Volition. Although all voluntary acts result from nerve impulses which have come from the motor areas of the cerebrum by way of the pyramidal tracts, we cannot suppose that they originate in the cells of the motor cortex. There is no evidence that these or any cortical cells are able to originate any activities whatever. All voluntary acts, as a matter of fact, are based upon associative memory; the immediate stimulus to the performance

of the voluntary act comes, not from the motor areas, but from that part of the association areas where the exciting memory is held. All memories, as we have seen, are at bottom retained sensory impressions. What happens, then, when we perform voluntary acts is that we cause to pass on to the motor areas stimuli which originally entered the nervous system by way of the receptors, and which have since been combined in various ways, and the resulting associations retained as memories. Voluntary acts are, therefore, the *completion* of *reflexes.*

The Usefulness of Associative Memory Depends on its Orderliness. It is perfectly obvio s that associations t be of value must be formed from related impressions or related concepts. We know that our brains normally form associations in this orderly way. How the brain is guided in its selection of material for making associations so as to include what is relevant and exclude the rest is quite beyond our knowledge or even imagination. That in the highly complex associative processes which we call thinking there may be a conscious selection or rejection of memories we know from our own experience.

It is true, of course, that the brain, being an imperfect instrument, often makes mistakes and forms associations that instead of being useful give rise to harmful activities. The resulting disaster, through the additional knowledge it affords, may enable the brain to form correct associations next time. Thus we profit by our mistakes.

The Interaction of Associative Memories. Inhibition. The human brain acquires in the course of years such a wealth of associative memories, based upon so many phases of experience, that the determination of the conduct to be employed in any particular situation becomes often a matter of much difficulty. One set of memories point toward one course and another set toward quite the opposite course. When this happens it is necessary to call in more and more remote considerations until the balance tips unmistakably in one way or the other. When even this procedure fails to be decisive, or when the mind wishes to avoid the labor of deciding by this method recourse is often had to a selective external stimulus. Deciding a course of action by the flip of a coin is a case in point.

Associative memories also come into conflict when immediate

considerations point toward one course and remote considerations toward a different one. Associative memories are classified by placing those of remote bearing higher than those of immediate bearing. Highest of all, because most remote, are abstract conceptions of right and wrong; conceptions of altruism, care for mankind, are higher than conceptions of family love; these in turn rank above purely personal considerations. Personal considerations which have regard to the future are higher than those dealing only with the immediate present. The progress of civilization is largely measured by the degree to which remote considerations outweigh immediate ones in determining conduct.

Because the cerebrum rests upon an underlying reflex mechanism the tendency of the organism is always toward immediate response to sensory stimulation; the hungry man tends to take the first food that comes to hand; the cold man tends to seek the nearest available shelter. The action of associative memory, when higher considerations dictate a different course, is to prevent or inhibit the carrying out of the immediate response. *Inhibition* is, then, one of the important functions of associative memory. The man who deliberately does what he knows to be wrong, acts as he does because his conceptions of right are not powerful enough to inhibit the response to the lower stimulus. The importance of inculcating the highest principles of right living by training and example, during the receptive period of the brain's development, is therefore clearly manifest.

Will Power. In some persons there is an inborn tendency to respond to immediate stimulation, even though associative memory shows that such response is not for the best. Such persons we describe as weak-willed. Those in whom the dictates of associative memory are supreme we call strong-willed. The weak-willed person yields to temptations which are powerless to move the one whose will power is great. In this definition of will power we have set associative memory against immediate stimulation, and usually the conflict is between these. Sometimes, however, the struggle comes between different immediate stimuli. In the weak-willed man the more insistent are likely to control, rather than the more important. If he is beseeched by various friends to accompany them different ways the most vociferous is usually the one to carry him off. The strong-willed man, on the other hand, makes his

decision on other grounds. On the other hand, various associative memories may be in conflict, and here again, whether obedience will be to the most clamorous or the most important depends on the strength of the will.

Cerebral Control of Inherent Reflexes. The exercise of the inhibitory function of associative memory as just described involves an ability on the part of the cerebrum to modify the reflexes of the lower parts of the nervous system. There is abundant evidence that such ability actually exists. It may be supposed to act through the discharge of impulses from the motor area which in some manner increase synaptic resistances in the course of the reflexes sufficiently to block them. A feature of the inhibition of inherent reflexes which points to this as the means of bringing it about is that in the case of sharp sensory stimulation the inhibition must be established before the stimulus is received. If one unexpectedly touches a hot object he inevitably jerks his hand away, but if he knew the object was hot, and nevertheless found it necessary to grasp it he could, through an act of volition, block his reflex path so effectively that the tendency to draw the hand away would be completely overcome.

The cerebrum is not invariably supreme in conflict with stimuli tending to cause automatic reflexes. When irritation of the throat or nasal passages is sufficiently pronounced coughing or sneezing will usually occur in spite of the strongest efforts to inhibit them.

The Development of Conditioned Reflexes. Habit Formation. By some means which we do not understand the repeated doing of something as the result of a given set of conditions results presently in the establishment of nerve paths of such ready passability that whenever the conditions recur the action is performed involuntarily. It is important to note that the antecedent conditions may be either particular sensory stimuli interacting with a complex group of associative memories, and operating at first wholly by volition, or may be trivial stimuli, at the beginning accompanying others that are significant, but later dissociated from them. After the reflex is once established the relation between stimulus and response becomes the same as in the inherent reflexes themselves. The nerve path is, however, probably always longer, involving some or even considerable areas of the cerebral cortex.

In ordinary parlance we speak of the establishment of condi-

tioned reflexes as habit formation.* Many of our habits are the result of deliberate repetition of particular actions when particular conditions obtain; others arise without our conscious participation, so that we may not know how they came into being. In either case, however, it appears that there has always been a repetition of definite stimuli antecedent to definite responses.

Useful conditioned reflexes are of the greatest value in our daily lives because on account of them many things that we have to do are more easily done than they would be if the whole mental process upon which the acts depend had to be gone through with at each repetition.

The tendency to habit formation can be used very effectively in training the child to right actions. It can be used as well in training to right thoughts, since thoughts are associative processes, and these tend to follow the lines laid down by habit.

Language. Of all the powers of the human mind its power to use language has had as much to do with the progress of the race as any other property it possesses. Language, from the standpoint of cerebral function, is simply a special sort of association; the association of arbitrarily selected sounds or written symbols with objects and concepts. Let us, for illustration, consider again the case of the child forming the concept mother. Coincident with the association of her voice, appearance, and other personal attributes into a definite concept is the repeated auditory stimulus of the word mother, heard when she is present or when she is indicated in some way. In course of time this particular succession of syllables is included as part of the concept. Several years later the group of written symbols making up the word mother is included in the same concept. Thus language, spoken and written, becomes indissolubly included in our whole mental equipment.

It is a curious fact that in man the use of language seems to be not optional, but a necessary factor in his mental development. Two lines of evidence favor this view. The first is the common experience of all of us that we are incapable of thought except in terms of words; coupled with the observation that no race of men

* The term habit is used here with reference to those acts which we do habitually because of having done them so often before, not with reference to habits which are based upon perverted or diseased conditions of the body, such as drug or liquor habits.

exists or is known to have existed without some form of language. The second, and more striking, fact is that certain regions in the association areas of the cerebrum appear to be specially devoted to language associations. Four such regions have been delimited more or less definitely, by studies of the physiological effects of their impairment through accident or disease. Two of these areas have to do with spoken, and two with written, language. One of the two areas for each form of language is sensory and the other motor. An interesting thing about these language association areas is that they seem to be confined to one of the cerebral hemispheres; in right-handed people the left hemisphere contains them, and in left-handed people they are said to occur in the right hemisphere. It has been observed, moreover, that the development of right- or left-handedness in infants is coincident with their learning to use language. Just what the relationship between the two properties may be is not clear.

Impairment of a sensory language area results in word-deafness or word-blindness; the sounds are heard, or the words are seen, but they are without meaning because the power to associate language with concepts is affected. When motor language areas are injured the power of expression is lost. The commonest of all these abnormalities is the loss of power to use spoken language, a condition known as *motor aphasia*. The sufferer from this condition knows what he wants to say but is unable to recall the words by which to express his ideas. Embarrassment often gives rise to a momentary inhibition of the motor aphasia region, resulting in the same inability to recall the needful words.

Since all our mental processes are dependent on language, impairment of the language areas would be expected to lower the whole mental power. This appears to be the case in most sufferers from this condition.

There is no evidence that any species of animals except the human species possesses the power to use language. This difference sets man sharply apart from the animals most nearly approaching him in intelligence.

Consciousness or Awareness. This is a phenomenon that we all recognize as existing in ourselves and as accompanying most although probably by no means all of our cerebral activities. That it is present when the cortical cells are actively functioning and

absent when they are inactive is indicated by the fact that any treatment, such as anæsthesia, which depresses nerve-cells, tends to abolish consciousness. It is a phenomenon whose nature is wholly unknown, and for whose existence, even, there is no objective evidence. We cannot prove that any lower animal, or any other person, for that matter, has the same sort of consciousness that we have. We can only suppose from the general similarity of their cerebral processes to ours that this particular phenomenon is also in them as in us. As we go down the animal scale where mental processes become simpler and simpler does it follow that consciousness becomes dimmer and dimmer? We ordinarily assume this to be true, but without any positive evidence upon which to base the assumption.

Emotions. The mental life as a whole includes two phases: the first is the intellectual phase, made up of associative processes, as described above; the second is the *emotional* phase about which a brief statement is now to be made. All of us realize that our emotions or feelings play a great part in our mental life. We are happy or unhappy, pleased or angry, satisfied or dissatisfied, and our behavior is commonly affected in accordance. The biological importance of the emotions resides in the fact just stated, that they influence behavior. This has been recognized, of course, for a long time, but only recently have we begun to see how the emotions are to be interpreted as factors in individual and racial welfare.

It is clear that the ultimate basis for feeling must be the same as for intellectual activity, *i. e.*, associative memory acting in co-operation with immediate sensory stimulation. We cannot have emotion without some cause; that cause must lie either in our present or past experience. Furthermore, emotion as human beings experience it, implies the function of consciousness. Through some means, not at all understood, our emotions operate as driving forces, impelling us to action in a way that purely intellectual processes never would. This is strikingly demonstrated in time of war, when it is thought necessary by the authorities to arouse the whole population to maximal effort, and extreme measures are adopted for the purpose of invoking hatred, and even contempt and disgust, for the enemy so that people will work and fight with enthusiasm, and not merely from a sense of duty.

A further important feature of emotion is that it operates to promote the efficiency of action, as well as to impel to its performance. The mechanism by which this is accomplished is described in the next chapter (p. 209). At this point all that will be said is that emotions are invariably attended by specific bodily manifestations, all strictly reflex, and in most cases clearly adaptive in that they rally particular energies essential to the efficient performance of the action to which the emotion tends. It must be admitted that not all the bodily effects attending emotions appear to be of this type, but enough of them are to justify us in stressing the phenomenon.

Cerebral Functions Compared in Man and Animals. In the higher animals as well as in man associative memory is the representative cerebral activity. So far as we can judge it represents in animals the climax of intellectual achievement. No animal has ever been seen to perform any act, not purely reflex, as are all "instinctive" actions, which associative memory cannot account for. The activities of man are for that matter based upon associative memory almost as fully as are those of animals. The important intellectual difference between man and animals is the possession by man of the faculty of *reason*, which is denied in large part to animals. The power to reason is itself, however, based upon associative memory. It may be roughly explained as the association of concepts whose relationship is not obvious. An animal, according to this idea, cannot reason efficiently because he cannot form associations except of concepts that manifestly belong together. The man reasons by perceiving relationships in apparently unrelated facts or ideas.

We must admit, however, that the most complicated acts of associative memory that have been observed in animals simulate so closely mental processes which in man are ordinarily thought of as reason, that no hard and fast limit of the latter can be set. We would scarcely venture to establish any point as marking the utmost intellectual achievement in animals, although we would not hesitate to say that in comparison with the possibilities of the human brain the extremest mental process of the most intelligent animal dwindles to insignificance.

The powers of using language and of highest reasoning are the only cerebral functions possessed by man and not by animals of

which we have positive objective proof. They are therefore the only ones of which physiology can take account at the present time. Physiology does not thereby deny, however, the existence of many activities in the human brain which are without counterpart in the brains of lower animals. While associative memory accounts completely for all non-instinctive actions of the lower animals, the history of the human race and the experience of individuals contain much that baffles explanation in terms of associative memory or of reason. The factors which lead the race always onward and upward to greater and greater heights of spiritual achievement are beyond the power of present-day physiology to analyze or even discuss.

Nourishment of the Brain. The cells of the cerebral cortex are very dependent upon their blood supply. A slight diminution in the rate of blood flow through the brain may depress the cortical cells to such an extent that consciousness is lost. The problem of retaining consciousness is, then, the problem of keeping the cerebral circulation up to the proper level. How this is accomplished will be discussed in connection with the circulation of the blood (Chap. XXII).

CHAPTER XII

LOCOMOTOR AND VISCERAL REFLEXES. THE AUTONOMIC NERVOUS SYSTEM

Locomotor Reflexes. So large a part of the process of adjustment of the higher animals to their environment consists of movements of the whole body from one place to another that we find a special set of reflexes present by which the necessary movements are accomplished. The particular characteristic of locomotor reflexes is that they involve the orderly interaction of a large number of muscles in obedience to sensory stimulation that is always complex, and often as complex as any to which the Body is called on to respond. An important problem in connection with locomotor reflexes is whether they are inherent, and so unconditioned, or acquired and hence conditioned. When we think of the apparent effort with which a child learns to walk we are inclined to assign the reflex immediately to the conditioned category. But further study raises doubts as to the correctness of such an assignment. For one thing, all the individual movements of which locomotion is compounded are known to be elicitable as inherent reflexes; furthermore, many quadrupeds, calves and colts for example, walk from birth, as do some bipeds, notably chicks. It is known that the brain in the human infant is not fully developed at birth; in fact regions believed to be of prime importance in locomotion do not begin to function till about the time when walking is usually learned. It has been argued by some that walking is an inherent reflex that appears as soon as all the nervous structures involved begin to function. It is impossible at present to state definitely for man whether the fundamental locomotor reflexes, walking, running, and leaping, are inherent or acquired. There is no doubt that they involve the brain; the more specialized locomotor reflexes of man, as swimming and riding a bicycle, can be considered conditioned reflexes with little probability of error.

The Sensory Basis of Locomotion. Locomotion takes various forms in individual animals and in different classes of animals. Walking, running, leaping, swimming, flying, these are all fun-

damental locomotor acts. With them must be classed also the more artificial forms of locomotion of civilized man, as bicycle riding or aviation. All these have certain primary features in common. They all require the accurately co-ordinated use of a number of muscles, and all of them involve the maintenance of *equilibrium*. More, in fact, than the simple maintenance of balance is involved. In every sustained locomotion there is constant restoration of an equilibrium that is continually disturbed. Of great importance for the guidance of co-ordinated muscular movement is a sense whose receptors are imbedded within the muscles themselves and distributed about the joints to which the contracting muscles impart movement. This is the *muscle* and *joint* sense, or briefly, *muscle sense*. Less well known than some of our other senses it is, as we shall learn (Chap. XIII), of equal rank with the others, and in connection with our muscular movements more important than most. Every bodily movement results in stimulation of the receptors of muscle sense. Any locomotor act is accompanied by a great stream of impulses from these receptors which serve not only to guide but to maintain the activity. There are definite organs of equilibrium, the semicircular canals and vestibule of the ear (Chap. XIV), by which the equilibrium sense is mediated. These two senses constitute the essential sensory basis for the locomotor reflexes. They are reinforced and modified by some of the other senses, notably touch and sight. Even when we are not paying attention to our walking movements we guide them unconsciously to a considerable extent by the touch of the feet on the ground whether in light or in darkness, and also largely by sight in the light.

Relation of the Cerebellum to Locomotion; Tonus. Underlying all skeletal muscle reflexes, but particularly reflexes of locomotion, is a state of instant readiness to function depending on the continued presence of a state of tonus (p. 135). A muscle that is excited to contract forcibly from a background of tonus operates under the mechanical advantage of having no slack to take up and no tissue elasticity to overcome before its action becomes effective. We have positive evidence that the nice co-ordinations so essential to efficient locomotor action are wanting if the tonus of the muscles is impaired. Tonus, as already pointed out, is a feeble sustained contraction of whole muscles maintained by full-strength te-

tanic contractions of a few fibers, acting in rotation. The stimulus to contraction is reflex, and depends primarily on afferent impulses aroused in receptors in the muscles themselves. These pass to the central nervous system where they are translated into efferent impulses so controlled and distributed as to throw successive small groups of fibers into contraction in turn. Tonus is in part a spinal cord reflex, but depends for its complete maintenance on an interaction of the cord with the *cerebellum*. Just how this latter structure plays its part is not known. There is, however, abundant evidence that locomotor reflexes are less well performed when the cerebellum is injured or destroyed, and also that the loss of efficiency is related definitely to an impairment in skeletal muscle tonus. Our next concern, therefore, is with the structure and connections of the cerebellum.

Structure and Connections of the Cerebellum. This organ, as shown in Figs 58–60 is a distinct portion of the brain, lying underneath the posterior part of the cerebrum, and behind and above the midbrain and medulla. It consists of a thin layer of gray matter superposed upon white matter, and having imbedded within the white matter at its base gray masses, the *nuclei* of the cerebellum. The thin outer gray layer, known as the *cortex*, is the region in which the incoming streams of sensory impulses are converted into outgoing streams of co-ordinated motor impulses. The cerebellum communicates with the brain stem, as, for convenience, the midbrain and medulla together are often called, by three pairs of stalks or *peduncles*. These consist of bundles of axons. The upper and lower stalks (Fig. 67) lead directly into the brain stem. The middle peduncles form the backward extension of the pons Varolii (Fig. 58).

The senses which are concerned with locomotor reflexes all have connection, either directly or by means of internuncial neurons, with the brain stem, and thence, by neurons whose axons extend through the peduncles, with the cerebellum itself. The anatomy of these paths is indicated in the last chapter (p. 181).

The *efferent* paths from the cerebellum, the paths over which pass the co-ordinated streams of impulses by which the cerebellum plays its part in maintaining skeletal muscle tonus, consist of chains of internuncial neurons. These begin in the cerebellar cortex and pass thence over the peduncles to the brain stem. A

particular mass of gray matter known, on account of its special coloration, as the *red nucleus* contains the terminations of most of the efferent cerebellar fibers. In the red nucleus connection is made with a second set of neurons which pass down the spinal cord (making up the *rubrospinal* tract) to final terminations in the ventral horn of gray matter in immediate synaptic connection with cell bodies of motor neurons. The cerebellum translates the total inflow of afferent impulses into a regulated stream of efferent impulses whose action is to co-operate with impulses entering the spinal cord directly from receptors in the muscles themselves in such a way as to maintain an effective tonus from which the ordinary contractions can proceed as from a base line.

Various other functions have been suggested from time to time for the cerebellum, and indeed it would be a matter of wonder if so large and apparently important a part of the brain should prove to have no other function than the maintenance of tonus. At present, however, the only way in which we can interpret the evidence at hand is as outlined above.

Postural Reflexes. In a previous chapter (p. 135) the dependence of posture on extensor tonus was mentioned. In the main the distinction between postural tonus and the tonus that characterizes all skeletal muscles is that the former is somewhat more forcible, indicating that more fibers are in contraction to maintain it. In man, with his erect posture, quite decided tension must be present to prevent the weight of the Body from causing the joints to sag. A striking fact about postural tonus is that it disappears promptly and completely when reflex or volitional contraction of the opposing muscles is evoked. The interrelation of neurons in the central nervous system is such that any stream of impulses tending to cause contraction of a flexor muscle plays also upon some of the synapses in the path of the tonus-maintaining impulses to the opposing extensors in such fashion as to suppress the latter stream completely (the interrelation is known as *reciprocal innervation* of antagonistic muscles).

The Brain Stem (Medulla and Midbrain). If our attention had been called to the matter when the courses of the various afferent and efferent pathways of the cerebrum and cerebellum were being described, we should have noted that the brain stem forms a great highway through which pass virtually all impulses

on their way to or from the higher brain structures. Moreover, most of the nerve tracts leading through the brain stem do not pass directly through, but suffer interruption in one or the other of the many nuclei which occur therein. Wherever a nerve tract is interrupted by a nucleus the axons leading into the nucleus terminate in synaptic connection with new neurons by which the tract is continued. There is always the possibility, where such connections are being formed, of a certain amount of diversion from the main channel into side channels. The medulla and midbrain, then, are strategically located for concentrating into small areas influences from all the receptors of the Body. This region has also its own efferent pathways. It affords, therefore, an additional field for the establishment of reflex arcs, but, as we shall see, of a somewhat less specialized sort than is afforded by the cerebrum.

There are a number of so-called "vital processes" going on in the Body. These are activities whose continuance is essential to the maintenance of life, and which must, therefore, go on quite independently of the will; they are of a sort, however, to require modification in accordance with the demands of the Body. Examples of such activities are the beating of the heart, breathing, the secretion of sweat.

Many of these so-called "vital" activities are really as purely reflex as any of the ordinary reflex acts of the Body, and those that are truly automatic are subject to constant reflex influence. Their immediate control is vested in certain *centers* located in the medulla. This location for the centers insures that they shall never be wholly free from sensory stimulation, for no matter how quiet the surroundings of the Body may be the processes going on within it give rise to sensory stimuli, and, as we have seen, whatever impulses are aroused are almost sure to pass through the brain stem. Detailed consideration of the various centers is not necessary here as each will be treated in connection with the vital process with which it is related.

The Autonomic or Sympathetic System. This system is treated as a distinct portion of the nervous system because to a rather special physiological function it adds peculiar anatomical relationships. In spite of its anatomical and physiological peculiarities, however, it forms an integral part of the whole nervous system,

and interacts with other parts as completely as though nothing distinugished it from them. Its old name has no present significance, having been given to it in the erroneous belief that its function is to bring remote organs into sympathy with each other. The name *autonomic*, by which it is at present known, signifies a mechanism not under voluntary control, and in thus emphasizing an important feature of the system, constitutes a more satisfactory designation. The special physiological function of the autonomic system may be stated in a sentence: it forms the efferent connection between the central nervous system and all the smooth muscles and glands of the Body, and the heart.

It will be recalled that the skeletal muscles have motor connection with the central nervous system by means of motor neurons, structures whose cell-bodies lie in the ventral horns of gray matter and whose axons extend directly to the muscles. The autonomic system differs from the motor system to skeletal muscles in that each pathway from the central nervous system to a smooth muscle or to a gland is made up of a sequence of two neurons. The first neuron has its cell-body in the ventral horn of gray matter; its axon passes out by way of the ventral root of the spinal nerve and the communicating branch (see p. 156) to one of the sympathetic ganglia where it forms synaptic connection with the second neuron of the chain. This neuron sends its axon back over the communicating branch to the spinal nerve along which it passes to its destination in a smooth muscle or a gland. Because of their positions with regard to sympathetic ganglia the first and second neurons are known respectively as *pre-ganglionic* and *post-ganglionic* neurons. The latter present the anatomical peculiarity of being for the most part devoid of myelin sheaths; nerve-trunks made up of post-ganglionic fibers can therefore be distinguished from other nerve-trunks by their gray color.

The structures innervated by the autonomic system perform their functions by acting to a considerable extent in groups together; not individually as do skeletal muscles. To enable them to be stimulated in groups single autonomic pathways commonly involve numerous end structures. This is accomplished by rich branching of the pre-ganglionic fibers, enabling each to have synaptic connection with a number of post-ganglionic neurons, and so to influence simultaneously numerous end organs.

The Effect of Nicotine. Much of our knowledge of the autonomic system has resulted from the discovery that application of the drug nicotine to sympathetic ganglia prevents the passage of impulses over whatever synapses may be contained therein. By the use of this drug, therefore, the point of contact of pre-ganglionic with post-ganglionic fibers in the pathway to any particular organ can be determined. To illustrate how its use brings out these points of contact we may take the autonomic innervation of the eye. The size of the pupil is regulated by opposing autonomic fibers; one set tending to constrict it, the other to dilate it. By the use of nicotine it has been shown that the contact of pre-ganglionic with post-ganglionic fibers in the constrictor pathway is in the ciliary ganglion, which is in the orbit, while for the dilator pathway the connection between pre-ganglionic and post-ganglionic fibers is in one of the sympathetic ganglia of the neck.

Reflex Control of the Autonomic System. The autonomic system, as we have seen, forms only the last step in the conducting pathway by which influences are brought to bear on the structures it innervates. Like the motor system for the skeletal muscles it conveys only those impulses which are imparted to it from without itself. It is, in other words, the efferent portion of a reflex mechanism.

The so-called "vital" processes of the Body are, with the exception of respiration, largely carried on through the agency of smooth muscles and glands. The autonomic system is, therefore, the system through which these processes have their nervous control. In the paragraph dealing with the brain stem the existence therein of reflex "centers" for the various "vital" processes was mentioned. On the afferent side these centers are subject to all sensory stimulations which affect the Body. On the efferent side they act through the autonomic system.

This reflex mechanism is not subject to voluntary control except for the single case of the muscle of accommodation of the eye, the *ciliary* muscle. This muscle is innervated through the autonomic system, but can be voluntarily controlled as completely as any muscle in the Body. (A few cases are on record of individuals who had voluntary control of the autonomic system to a considerable extent.) When we say that the autonomic system is not under voluntary control we are simply stating in other words that the

motor area of the cerebrum is not able to establish connection through the pyramidal tracts with the neurons of this system. Since this system is outside the control of the motor area all reflexes which affect it must be immediate ones. Only present stimuli can arouse it to activity. When we bear in mind that the proper functioning of the Body requires its vital activities to be adjusted to its immediate circumstances and not to its circumstances of a week or a year ago, the necessity that autonomic reflexes be immediate is manifest.

Grand Divisions of the Autonomic System. Not all parts of the central nervous system give rise to autonomic pre-ganglionic neurons. A group originates in the brain stem. Its fibers are distributed through cranial nerves. These are called *cranial* autonomics. The vagus nerves (p. 160) consist largely of cranial autonomic fibers distributed to various organs of the trunk. A second group arises in the thoracic and lumbar regions of the spinal cord. These are distributed through the sympathetic system of the old classification. They are known as *thoracico-lumbar* autonomics. The third group of fibers arises in the sacral portion of the cord. These are distributed to the pelvic region and constitute the *sacral* autonomics. It is customary to use the old term "sympathetic system" to apply strictly to the thoracico-lumbar subdivision, and the term "parasympathetic system" to apply to the cranial and sacral divisions together.

In a previous paragraph (p. 126) attention was called to the peculiar feature of smooth muscle, shared by heart muscle, of requiring double innervation. These tissues must have stimulation to augment their activity and other stimulation to inhibit it. Both sorts of innervation are furnished through the autonomic system. An important feature of the system as a whole is that the opposing innervations to any organ come to it ordinarily by way of different grand divisions. The cranial and sacral groups stand in opposition to the thoracico-lumbar group. It does not follow that one grand division is always inhibitory and the other augmentory. As a matter of fact the thoracico-lumbar system augments some activities and inhibits others. Whichever are augmented by the thoracico-lumbar are inhibited by the cranial or sacral, and vice versa.

Significance of Sympathetic and Parasympathetic Functions. During the ordinary life of the individual the balanced action of

the opposing subdivisions of the autonomic system serves to carry on the normal quiet functioning of the maintenance mechanisms of the Body, which, as stated previously (p. 207), are operated by smooth muscle. As we study in detail these structures in later chapters we shall see how admirably through this balancing of opposing innervations they are kept in just the desired degree of activity.

In addition to this, which we may call its routine function, the sympathetic system proper shows a special, and very significant, property which can be made clear through a tabulation of a few of the many bodily changes governed by the autonomic system, with the respective parts played by the sympathetic and parasympathetic systems set down.

	Sympathetic	*Parasympathetic*
Pupil of eye	dilated	contracted
Salivary secretion	inhibited	excited
Hair	erected	depressed
Blood vessels of skin	constricted (pallor)	dilated (flushing)
Heart	accelerated	slowed
Digestive organs	inhibited	excited (to normal activity)

If we consider an individual whose pupils are dilated, whose mouth is dry, whose hair tends to stand on end, whose face is pale, whose heart is racing, and whose stomach is a leaden weight within him we have no difficulty in recognizing the picture. Only terror, rage, or sharp pain could bring about precisely this condition. We have then in this property of reacting characteristically to conditions involving strong emotions a feature of the sympathetic system.

This an Emergency Mechanism. At first thought there may appear little utility in the characteristic reactions of excitement described in the last paragraph. If we note, however, that the conditions that arouse these reactions are such as call for a rallying of the Body for flight or struggle we begin to see wherein the importance of this mechanism lies. In general its effect on the Body is a *diversion of resources from the maintenance organs to those of external adjustment,* the latter making up the mechanism on which the Body must depend for salvation in time of stress. The dilation of the pupil may be supposed to widen the angle of vision. The dryness of the mouth signifies that energy ordinarily employed in

producing saliva is now set free for use elsewhere. The erection of the hair, of no importance in man, is in many of the lower animals an important part of the scheme of defense. The pallor of the face is the result of the diversion of blood from the skin, whence it can be spared, to the muscles and brain where it is greatly needed. The acceleration of the heart results in a quickened circulation of blood through the regions of heightened activity. The inhibition of the digestive organs is another example, like the cessation of salivary secretion, of the suspension of functions not immediately essential, in order that all the bodily energy shall be available for the emergency. Numerous other reactions of the sympathetic mechanism also contribute to the general plan of defense. These we shall examine in due course. Here we need only note that all of them tend toward increasing the efficiency of the skeletal muscles and the central nervous system, which together make up the emergency mechanism.

The Relation of the Autonomic System to Emotional States. In a previous paragraph (p. 199) the fact was noted that emotion in general is accompanied by activity of the autonomic system. We have just examined the basis for this relationship in those emotions that are associated with the immediate need of self-preservation. An interesting fact, and one of great practical importance, is that the emotion of worry or anxiety, which is responsible for much of the discomfort of life, has significance as a means of preparing *before hand* for a time of trouble. We may describe it as an anticipatory emotion. We bring about in our Bodies through worry the characteristic reactions of the sympathetic system. Unfortunately, these reactions, useful indeed when the actual stress is at hand, are inimical to the carrying on of the ordinary bodily processes, so that their occurrence in advance of the emergency does no particular good, and when, as usually happens, the worry proves to have been needless, real harm.

Emotion of satisfaction and contentment appear to manifest themselves chiefly through the cranial autonomics. The sacral autonomics control the activities of the generative organs. Their emotional associations are for the most part those concerned with reproduction.

Neuro Muscular Fatigue. In a previous chapter (p. 119) muscular fatigue was discussed, and shown to be due to the accumula-

tion of lactates in the muscles. General bodily weariness was also spoken of, the suggestion being made that it is also attributable, at least in some cases, to the effects of accumulated lactates on sensitive tissues. A fact of considerable importance is that in the ordinary working of the Body the muscles are protected from becoming exhausted by a precurring fatigue which develops in the nervous system and acts as a block to the further passage of impulses to the muscle fibers threatened with exhaustion.

Two general locations are recognized in the nervous system for the occurrence of fatigue. The first of these is in the synapses. The delicate junctions between neuron and neuron are believed to be highly suspectible to fatigue. In terms of the prevailing theory we would say that the accumulation of waste products at the synapses increases their resistance to the passage of nervous impulses, and that the resulting hindrance to nervous action constitutes fatigue. The second place of fatigue is at the junctions between motor nerves and the fibers of skeletal muscle. These junctions consist of minute flat plates pressed against the muscle-fibers and in which the nerve-fibers terminate. They are known as *motor end plates*. There is ample proof that as the result of continued excitation of a muscle the neuro muscular junctions show a falling off in the ease with which impulses pass through them to muscle-fibers. Synaptic fatigue and end plate fatigue occur in such minute structures that we would be apt to expect recovery to be rather rapid. As a matter of fact quick recovery seems often to occur. It is a common experience to obtain marked relief from fatigue by the briefest sort of a nap. Nevertheless, we are bound to recognize that although the *feelings* of fatigue may be quickly dissipated actual restoration of the fatigued structures requires time. An ordinary night's rest is none too long for recovery from nervous fatigue. In fact there is definite evidence that under many conditions a single night's sleep does not suffice for complete restoration. The almost universal and very valuable habit of abstaining from ordinary duties one day in seven has its physiological significance in the necessity of allowing at intervals a longer period of restoration than the usual nightly ones, in order that any fatigue which failed to be overcome in ordinary course might be got rid of therein. That this longer rest period be spent in sleep is no means always desirable. When we recall that the synapses

which experience fatigue primarily are the ones that are being *used* we realize that the essential for rest is often *diversion* rather than sleep. During the rest periods one's mental activities should be along as different lines as possible from those of his ordinary workaday life. Thus his fatigued synapses can be resting while others are busy. This same fact emphasizes the importance of *diversity* of *interests*. Where one's thoughts cling in certain ruts mental fatigue is apt to be more pronounced than where various lines can be followed. In those whose occupation requires prolonged concentration it is particularly advantageous to have widely different interests to turn to during the intervals of relaxation.

Hormones of the Nervous System. Adrenin. (Known also as Epinephrin.) This hormone has a variety of bodily effects. At this point stress will be laid on its action on nervous structures; other effects are described later (p. 399). The hormone is interesting chemically because it was the first to be obtained pure, and so to be studied from the chemical standpoint. It is a complex organic compound, containing carbon, hydrogen, oxygen and nitrogen. A remarkable fact about it is the very great dilution in which it is active; one part in five hundred million produces demonstrable effects. The hormone is manufactured by cells of a definite sort, making up the so-called *chromaffin tissues*. These are found in minute masses in various regions of the Body, and in quantity in the *adrenals*.

The Suprarenal Capsules or Adrenals are a pair of small organs weighing together about 12 grams (½ oz.) placed one on top of each kidney. They have, however, no intimate connection with the kidneys, and in many animals are placed at some distance from them. Each consists of a denser less colored external *cortex*, not composed of chromaffin tissue and in fact a distinct endocrine gland functionally, and a central deep yellow-brown *medulla*, which is composed of chromaffin tissue and is the source of the adrenin. The medulla is richly supplied with sympathetic (thoracico-lumbar autonomic) nerve fibers.

The Action of Adrenin. Careful studies have shown that adrenin is present in the blood under ordinary circumstances in almost inconceivably minute amounts; too minute, in fact, to evoke any except the most delicate of the effects of which the hormone is capable. Our detailed knowledge of the functioning of adrenin

has been gained chiefly by observing the results of its introduction into the blood in larger than normal amounts. The Body responds to these enlarged doses by a considerable number of very definite reactions which, when first observed, seemed to be quite unrelated, but are now recognized as combining to bring about a particular bodily condition, and one which, as we shall see, is sometimes of great importance to the organism. Not all these effects of adrenin can be described in this place, some will have to be deferred to later chapters; but enough can be presented to make clear the significance of its action.

One of the properties of adrenin is to stimulate chemically the terminations of the thoracico-lumbar autonomic system. It is thus able to bring about the same bodily reactions as are called forth through thoracico-lumbar autonomic activity. Dilation of the pupil, acceleration of the heart, constriction of the blood-vessels, with consequent heightened blood pressure, all are brought about by the injection of adrenin into the Body. These manifestations, as we saw above, are part of what we have described as the *emergency reaction* of the Body, and the ability of adrenin to bring them about reveals its function as the *emergency hormone.* The emergency reaction is so vital in time of stress that the Body does not depend wholly on the nervous system to evoke it. The action of the thoracico-lumbar autonomics is reinforced by the chemical stimulation of adrenin. This adrenin action depends, as we have seen, on the presence in the blood of larger than normal amounts of the hormone. The adrenal bodies are under the control of nerves which form part of the thoracico-lumbar system. Whenever, in a time of excitement, there is an outrush of impulses over this system, the adrenals are stimulated to great activity, and pour out their product into the blood stream. Thus at the time when increased adrenin is advantageous to the organism it is provided. The persistence of the bodily effects of strong emotion after the emotion itself has subsided may be explained by the continued presence of adrenin in the blood.

The reinforcement of the thoracico-lumbar autonomic mechanism is only one phase of the emergency function of adrenin. Another, and very interesting, feature of its action is in connection with the fatigue of the neuro-muscular junctions described in an earlier paragraph (p. 210). We saw there that the effect of fatigue

on these junctions is to make the passage of impulses over them difficult. Recently the important discovery has been made that adrenin has the property of counteracting this fatigue, and thus making the muscles more accessible to nervous impulses. The value of this property in time of emergency is obvious. It explains a familiar fact that was unexplained before, namely, the "strength of desperation." Why a man in a tight place should suddenly experience an access of strength we now suppose to be because in connection with the powerful emotions engendered by his situation there is an outpouring of impulses over his thoracico-lumbar autonomic system. His adrenal bodies are stimulated thereby to abundant production of adrenin; the adrenin is carried by his blood to all his muscles, and there makes the access of nerve impulses to the muscles more ready. The gain is not in actual muscular strength, but in ability to use to the full the strength already present.

The Thyroid. This organ lies in the neck on the sides of the windpipe and consists usually of a right and a left lobe united by a narrow isthmus across the front of the air-tube. It is about thirty grams (one ounce) in weight; in the disease known as *goiter* it is greatly enlarged and its structure altered. The thyroid is dark red in color and very vascular, richly supplied with nerves, and is subdivided by connective tissue into cavities or *alveoli*, the largest of which are just visible to the unaided eye. Each alveolus is lined by a single layer of cuboidal cells, and filled by a glairy fluid known as the thyroid colloid.

Thyroxin. From the gland can be obtained, in addition to the usual organic compounds, a peculiar substance containing a large percentage of iodin, and known as *thyroxin*. The substance is an iodin compound of a complex nitrogen-containing organic acid. It is undoubtedly the pure hormone. The thyroid produces it steadily at the rate of about 0.2–0.4 milligram (one milligram equals 0.000035 oz.) daily, making good a daily loss of an equal amount. The total quantity in the Body at one time is estimated to be about 12–14 milligrams. If the thyroid is overactive, so that more than this is present at once, the condition is called *hyperthyroidism;* if underactive, so that the Body contains less than the normal quantity, the condition is *hypothyroidism*. Definite symptoms ensue from either of these conditions; they are described in part below.

Dependence of Thyroid Function on the Iodin Supply. In order to manufacture its due quota of thyroxin the thyroid must obviously have at command sufficient supplies of all constituents of the hormone. It happens that iodin, the constituent to which the substance owes much of its special character, is sparingly present in Nature, except in the ocean, where it occurs in great dilution, but nevertheless on account of the vast size of the ocean in enormous total amount. Many sea plants are quite rich in iodin, taking it up little by little from the surrounding water. As these plants die their remains settle to the bottom and decompose, leaving in the detritus iodin compounds among other things. Much of the present land surface was in past geologic time beneath the sea and became more or less impregnated with iodin salts. Thus land plants and land animals have a source of supply.

Although there is a steady loss of thyroxin from the bodies of all men and higher animals the iodin given out is not wholly wasted; much of it finds its way into the water or soil to be picked up again by plants and so made available again for the use of animals. However, if the population in any area remote from the sea increases greatly there may not be enough iodin to go around; continued cultivation of the soil leaches out the iodin salts and thus acts also to deplete the supply in populated districts. Near the ocean enough iodin is carried in wind-blown spray to make good the demands, even of dense populations. The fact has become increasingly manifest, however, that shortage of iodin is a real factor in affecting the health of inland populations. Any individual who suffers from shortage necessarily develops hypothyroidism of greater or less severity, according to the extent of the shortage.

Goiter. Persons otherwise normal, but failing to obtain adequate supplies of iodin, frequently experience overgrowth (hypertrophy) of the thyroid gland, known as simple (or endemic) goiter. The overgrowth is obviously a compensatory reaction; since cells of normal size are not able to produce enough of the hormone a stimulus is set in operation causing them to enlarge. Of course the compensation is ineffective in the absence of adequate supplies of iodin, and symptoms due to hypothyroidism are manifest to some degree in nearly all sufferers from goiter.

Function of Thyroxin. The fundamental action of thyroxin is to act as hydrogen transporter in resting cells. In other words,

the underlying energy-yielding reactions of basic metabolism (p. 26) are dependent in part on the presence of this hormone. The large effects of this action are discussed in a later chapter (p. 545). Here their relations to the nervous system are to be considered. In nerve cells as in other cells the efficiency with which active function is carried on depends very largely on the condition of readiness in which the cells are maintained by their basic metabolism (p. 28). In the case of nerve cells there appears to be a narrow margin of efficient basic oxidation; if the oxidation falls below this margin the nervous functioning becomes sluggish and ineffective; if the oxidation rises above the margin nervous action becomes more or less uncontrolled and erratic. Thus for efficient nervous function it is highly important that the amount of thyroxin be neither too small nor too great.

Hypothyroidism. The nervous symptoms attributable to insufficient amounts of thyroxin in the Body range from slight decrease in mental alertness to complete idiocy, according to the extent of deprivation. Hypothyroidism due solely to insufficient iodin in the diet is rarely serious, because no regions occupied by man are completely devoid of iodin. Marked symptoms are due to failure of the thyroid gland to function properly. The failure may be due to disease, or in a small percentage of cases to congenital deficiency, due to heredity. Obviously deficiencies in the thyroid, whether arising from disease or by heredity, produce more marked symptoms in regions short of iodin than elsewhere, the combination of deficient thyroid and iodin shortage accentuating the difficulty of manufacturing sufficient thyroxin.

Congenital thyroid deficiency manifests itself shortly after birth; the unfortunate sufferers develop into dwarfish, misshapen idiots unless given thyroxin treatment as described below. This condition is known as *cretinism*, and the sufferers are called *cretins*. Disease of the thyroids developing later in life gives rise to *myxedema*, with symptoms similar to but usually less severe than in cretinism, and calling for similar treatment.

Treatment with Iodized Salt and with Thyroxin. With the discovery that simple goiter is due to shortage of iodin in the diet, and with the further observation that the amounts needed are almost infinitesimal, a means of relieving the situation at once suggested itself, and has been put into rather widespread application. The

method is to add small concentrations of sodium iodid to ordinary table salt at the refineries. So little need be added that the expense is nominal; and the presence of the iodid is imperceptible to the sense of taste. The results have been gratifying, and promise, indeed, to solve the problem of iodin shortage in civilized communities the world over.

Administration of iodin cannot be expected to be particularly beneficial in cases of actual failure of thyroid function. When the thyroid is unable to manufacture thyroxin in sufficient amount the deficiency is made good by administration of the hormone directly. Fortunately it is not necessary that pure thyroxin be employed. Thyroid extracts, in which the thyroxin is mixed with other organic substances, can be prepared much more cheaply than can the pure hormone. Passage through the digestive tract does not injure this extract; consequently it can be given by mouth, as part of the diet. There are many cases on record of marked benefit, amounting often to complete cure, even in severe hypothyroidism. The improvement lasts, of course, only as long as administration of thyroid extract is kept up. Should treatment be allowed to lapse a return to the former state would inevitably ensue, unless in the meantime the thyroid had recovered function. In congenital hypothyroidism (cretinism) there is unfortunately often a more widespread abnormality than simple thyroid deficiency, and in cases thus complicated treatment with thyroid extract has given less benefit than hoped, but in the absence of complications the same beneficial results follow in cretins as in cases of noncongenital hypothyroidism.

Hyperthyroidism. There is a disease known as exophthalmic goiter (Graves's disease), named from the protrusion of the eyes which is a prominent symptom. This disease is due to an increase in the amount of the thyroid hormone (or sometimes to a chemical change whereby it becomes more potent). The effects on the Body are just the opposite of those seen in myxedema. There is heightened nervous activity, often proceeding so far beyond the normal as to constitute mental instability. One of the triumphs of modern surgery is the establishment of a method whereby enough of the thyroid can be removed to reduce the hormone to normal amount, and so cure the complaint.

CHAPTER XIII

THE RECEPTOR SYSTEM. INTERNAL AND CUTANEOUS SENSATIONS

The Receptor System constitutes the Body's means of gaining information of its surroundings and of such internal conditions as it needs to know about. Since the surroundings may play upon the Body in many different ways and through the operation of many forms of energy, receptors are provided which respond to various sorts of stimuli. Inasmuch as proper adaptation requires that different sorts of stimuli affect the Body differently, particular receptors are specialized to respond most readily to particular kinds of stimulation. Stimuli are, as already pointed out (p. 30), energy changes of one sort or another. An interesting fact about the receptors is that while most of them are primarily specialized to respond to particular kinds of energy change, many of them can be aroused by other kinds as well. When a receptor is stimulated it gives rise in turn to a stream of nervous impulses which passes into the central nervous system and is distributed therein according to the paths that are open to it. Recent study has shown that the impulses passing in from one type of receptor may differ in minute details from those passing in from another. These minute differences are probably important in determining which of the many potential paths through the spinal cord and brain shall be followed by impulses arising in particular receptors. The important point to be kept in mind is, however, that the response of the organism is not determined by the special character of the stimulus, but by the path through the nervous system followed by the nerve impulses which the stimulus arouses. It is necessary to make this distinction at the very beginning of our study of receptors because in us receptor stimulation commonly arouses conscious sensations and we learn by experience in early childhood that the kind of sensation depends nearly always on the character of the stimulus. The result is that we naturally think of sensations of light in terms of light itself and not in terms of an impulse stream passing in from the eyes. When we discover, as many of

us do, that sensations of light can be aroused by pressure on the eyeball we are at a loss to explain the fact until we learn that the type of sensation depends on the part of the cerebrum to which the impulses are conveyed (p. 185), and not on the sort of stimuli by which they are evoked.

Receptor Stimulation does not Invariably Arouse Sensation. When a receptor is stimulated and a stream of nerve impulses called forth several things may happen as the result. Immediate reflexes may ensue; memory may be established; associative processes of various degrees of complexity may be set in motion; sensations may be aroused. Every effective receptor stimulation brings about some one or more of these results. It by no means follows that all of them are evoked every time a receptor is thrown into action. Particularly important is it for us to realize that conscious sensation does not have to occur in order that the receptors and the nervous system may function successfully. As a matter of fact we do not know positively that such things as sensations are experienced by other than human beings; we infer with much probability that many lower animals also experience them; few would hold that the lowest forms in which receptors occur have sensations in the sense in which we have them.

The Differences Between Sensations. Although for the reasons just stated undue prominence should not be given to the sensations when receptors are being studied, as here, from the physiological point of view, there are some things about sensation that need to be known in order to appreciate the operation of the receptors. The present paragraph and the one following are devoted to these.

We distinguish among our sensations kinds which are absolutely distinct for our consciousness, and not comparable mentally. We can never get confused between a sight, a sound, and a touch, nor between pain and hunger; nor can we compare them with one another: each is *sui generis*. The fundamental difference which thus separates one sensation from another is its *modality*. Sensations of the same modality may differ; but they shade imperceptibly into one another, and are comparable between themselves in two ways. First, as regards *quality:* while a high and a low pitched note are both auditory sensations, they are nevertheless different and yet intelligibly comparable; and so are blue, purple, and red objects. In the second place, sensations of the same

modality are distinguishable and comparable as to amount or *intensity:* we readily recognize and compare a loud and a weak sound of the same pitch; a bright and feeble light of the same color; an acute and a slight pain of the same general character. Our sensations thus differ in the three aspects of *modality*, *quality within the same modality*, and *intensity*.

As regards modality, we commonly distinguish five senses, those of sight, sound, touch, taste, and smell; to these at least six others must be added to make the list approximately complete. These additional senses are temperature, pain, hunger, thirst, muscle sense, and equilibrium sense. The last five of this list were formerly set apart as *common sensations*, but there seems to be no good reason for viewing them in any different light from the others.

The Psychophysical Law. Although our sensations are, in modality or kind, independent of the force exciting them, they are not so in degree or intensity, at least within certain limits. We cannot measure the amount of a sensation and express it in foot-pounds or calories, but we can get a sort of unit by determining how small a difference in sensation can be perceived. This smallest perceptible difference varies in the different senses and for different amounts of stimulation in the same sense. Its variation in any single sense follows, however, a certain law. *The increase of stimulus necessary to produce the smallest perceptible change in a sensation is proportional to the strength of the stimulus already acting;* for example, the heavier a pressure already acting on the skin the more must it be increased or diminished in order that the increase or diminution may be felt. Examples of this, which is known as *"Weber's"* or *"Fechner's psychophysical law"* will be hereafter pointed out, and are readily observable in daily life; we have, for example, a luminous sensation of certain intensity when a lighted candle is brought into a dark room; this sensation is not doubled when a second candle is brought in; and is hardly affected at all by a third. The law is only true, however (and then but approximately), for sensations of medium intensity; it is applicable, for example, to light sensations of all degrees between those aroused by the light of a candle and ordinary clear daylight: but it is not true for luminosities so feeble as only to be seen at all with difficulty, or so bright as to be dazzling.

Besides their variations in intensity, dependent on variations

in the strength of the stimulus, our sensations also vary with the irritability of the sensory apparatus itself; which is not constant from time to time or from person to person. In the above statements the condition of the sense-organ and its nervous connections are presumed to remain the same throughout.

Classification of Receptors. It is possible to group the sense-organs in several different ways according to the properties upon which the classification is based. If we group them according to the forms of energy to which they respond they fall into four classes: 1, the senses aroused by *mechanical* stimulation, touch, pain, hunger, muscle sense, equilibrium, and hearing; 2, those aroused by *chemical* stimulation, taste, smell, and probably the sensation of thirst; 3, the temperature sense, aroused by *thermal* stimuli; 4, the sense of sight, aroused by stimuli of *light.*

A second classification is based on the position of the receptors in the Body. This classification gives us three main groups: 1, the *extero-ceptors,* located at or near the surface of the Body, and stimulated by external energy-changes; 2, *proprio-ceptors,* located within and among the body-tissues, and stimulated by energy-changes arising within the organism; 3, *intero-ceptors,* located in the lining of the alimentary tract, and stimulated by conditions present in that tract (the justification for making the intero-ceptors a distinct group is that strictly the digestive cavity is an inclosure of the exterior within the Body, and its lining therefore an external surface; but since the external environment can affect the region only indirectly its receptors are not properly extero-ceptors, and so must be placed in a class by themselves).

A third classification attempts to group the receptors in accordance with the types of reflex responses they evoke. This classification is limited in its scope, since many of the receptors elicit a wide variety of responses. There are, however, three quite definite classes worthy of note. The first includes receptors that elicit *self-protective* responses. In man, and by inference in higher animals, sensations of pain, or irritation, as itching or tickling, or discomfort, as nausea, ordinarily accompany stimulation of receptors of this class; the effects tend to be noxious in all organisms, whether able to perceive the sensations or not; Sherrington has accordingly suggested the term *noci-ceptor* to apply to members of this group; the advantage of the term is that it avoids implications of con-

scious sensation, a desirable thing in classifications of receptor organs. The second class includes receptors whose main effect is to determine and regulate *postural tonus;* receptors in muscles and tendons, and about the joints (commonly known as organs of muscle-and-joint sense) and the equilibrium receptors in the ear, make up this class. The third class includes receptors that tend to cause the organism to seek for and take food or water; receptors that ordinarily arouse sensations of hunger and thirst are included. Our better-known sense organs, those for vision and hearing and the organs of touch, smell, and taste contribute more or less impartially to all these responses, as well as to the elicitation of many others that do not fall directly in any of the three groups; no satisfactory classification according to this scheme is possible for them.

Receptors Assigned to Definite Classes. The most satisfactory of the three schemes of classification given above is the second, which groups the receptors according to their position in the Body. Under the head of extero-ceptors come two sub-groups, the *contact receptors* and the *distance receptors.* The contact receptors are those of pressure (touch), noxious irritation of the skin (pain, itching, tickling), temperature change (warmth and cold); the distance receptors are the organs that react respectively to odorous substances in the air (smell), to a particular range of vibrations of matter (hearing), and to light (vision).

The proprio-ceptors include those that mediate pressure in muscles and tendons, about the joints, and elsewhere within the Body except in the alimentary tract, noxious irritation within the Body, pressure receptors in the equilibrium organ of the ear (semicircular canals and vestibule).

The entero-ceptors include organs that react to sapid substances in the mouth (taste), to decrease in the amount of water in the mucous lining of the throat (thirst), to special contractions of the stomach-walls (hunger), and to irritating motions of the stomach and intestines (nausea).

The above order of classification is not followed in the discussion of the various receptors. Instead the less well-known are described first, leaving those that are most familiar, and as it happens also most complicated, to the end.

Not Included in the Classification are a group of feelings which *in consciousness* have features in common with the senses,

although not known as yet to depend on the operation of definite receptors. Examples are *fatigue* and the general state of ill-feeling called *malaise*. It is also questionable whether all types of *headache* are mediated by receptors. A characteristic of all these feelings is that they are recognized in consciousness as bodily states, corresponding in this regard to the sensations aroused by the proprio-ceptors and entero-ceptors, but not by the extero-ceptors save in two special instances, pain, and coldness or warmness of the Body as distinct from the same properties in external objects. To illustrate the difference in consciousness between receptor stimulation referred to bodily states and to external objects suppose that a knife is held in the hand. The sensations we have are referred in our consciousness to the knife. It is hard, cold, etc. Let the knife now cut through the skin. The stimulus arises from the knife as much as before, but it is to the hand and not to the knife that we refer the feeling of pain.

The Muscle Sense. From the muscles arise sensations of great importance, although they do not often become so obtrusive in consciousness as to arouse separate attention. They are due to the excitation of sensory nerves arising from receptors within the muscles themselves, or in the tendons or joints with which the muscles are connected.

We have at any moment a fairly accurate knowledge of the position of various parts of our Bodies, even when we do not see them; and we can also judge fairly accurately the extent of a movement made with the eyes shut. The afferent nerve impulses concerned in the development of such judgments may be various; different parts of the skin are pressed or creased; different joints are subjected to pressure; different tendons are put on the stretch and different muscles are in different states of contraction, and it is by no means easy to determine the part played in each case by the sensory nerves of the different organs. Moreover, when we push against an object, or lift it, we are able to form a judgment as to the amount of effort exerted; but here again pressure on skin and joints and tension of tendons come in. Although under normal circumstances the skin sensations are undoubtedly of importance, they are not necessary: persons with cutaneous paralysis can, apart from sight, judge truly the position of a limb and the extent of movement made by it; and in many movements change

in joint pressure must be very little if any. We have then to look to muscles and tendons themselves for an important part of the sensations, and in both muscles and tendons there are organs in connection with nerve-fibers which are certainly sensory in nature: moreover, muscle sensory nerves appear to be excited by mere passive change of form in the muscle; with the eyes closed each of us can tell quite accurately how much another person has lifted one of our arms.

Of much greater importance than the conscious sensations we experience from stimulation of the muscle-sense receptors are the reflexes mediated by them. We need here only remind the reader that tonus, an essential underlying feature in nearly all reflex activity, and the main factor in maintenance of posture, depends largely on muscle-sense stimulation (p. 203); furthermore the co-ordinated interaction of the muscles in locomotion is also dependent to a marked extent on impulses from these same receptors. The proof of these statements is in the fact that interruption of the *afferent* paths from the muscles, without any impairment whatever to the *motor* paths to them, practically abolishes tonus, and interferes also with the co-ordinative actions of locomotion.

The sensations by which we judge the extent of a muscular movement are so delicate that we can distinguish very minute differences of contraction; the ocular determination of the distance of an object not too far off to have its absolute distance determined with considerable accuracy, depends almost entirely upon judgments based upon very small changes in the degree of contraction of the internal and external straight (*recti*) muscles, converging or diverging the eyeballs (p. 301). A singer, too, must be able to judge with great minuteness the degree of contraction of the small muscles of the larynx necessary to produce a certain tension of the vocal cords. It may be well to point out that in making these judgments we do not refer the sensation to any given muscle or muscles; it is merely associated with a certain movement or position, and a person who knows nothing about his ocular muscles can judge distance through sensations derived from them, quite as well as any anatomist. This fact is of course correlated with the fact that in voluntary movement we do not make a conscious effort to contract any particular muscles: the higher nerve-centers are merely concerned with the initiation of a given move-

ment of a given extent, and all the details are carried out by lower co-ordinating centers. In ordinary daily life in fact we have no interest whatever in a muscular contraction *per se:* all we are concerned with is the result, and consciousness has never had need to trouble itself, if it could, with associating a particular feeling or a particular movement with any individual muscle.

Muscular feelings are, as already pointed out, frequently and closely combined not only with visual but also with tactile, in providing sensations on which to base judgments: in the dark, when an object is of such size and form that it cannot be felt all over by any one region of the skin, we deduce its shape and extent by combining the tactile feelings it gives rise to, with the muscular feelings accompanying the movements of the hands over it. Even when the eyes are used the sensations attained through them mainly serve as short-cuts which we have learned by experience to interpret, as telling us what tactile and muscular feelings the object seen would give us if felt; and, in regard to distant points, although we have learnt to apply arbitrarily selected standards of measurement, it is probable that distance, in relation to perception, is primarily a judgment as to how much muscular effort would be needed to come into contact with the thing looked at.

Hunger. In discussing this sense we must first draw a distinction between true hunger and appetite. The latter is a feeling that food would be acceptable, with usually a degree of pleasurable anticipation included. It is often heightened by the odor and taste of food. There is reason to doubt whether appetite should be called a sense in the strict meaning of that term. It might, perhaps, be better classed with fatigue and the other feelings mentioned in a former paragraph as not representing the results of definite receptor stimulation. True hunger, on the other hand, is a definite sense aroused in a specific manner. In consciousness it takes the form of sensations arising from the stomach, which, when pronounced, are of a character sufficiently disagreeable to justify their description as "pangs of hunger." During a period of hunger the feeling is not continuous, but comes and goes, usually at fairly regular intervals. By means of interesting experiments, in which records were obtained of the movements of the stomach, the fact was demonstrated that spasms of hunger are the result of vigorous contractions of the muscular walls of the organ. Apparently these

contractions stimulate, mechanically, receptors imbedded in the stomach walls. Most of the facts about hunger are readily explicable in accordance with this idea of its nature when we recall that the stomach, whose contractions evoke the sensations, is governed by the autonomic system, which, in turn, is subject to emotional as well as to reflex influences. The well-known capriciousness of hunger can thus be accounted for. If the need for food were the necessary incitement to hunger we should expect the greatest hunger to be after the longest fast, but the experience of a great many people is that their least hunger before any meal is before breakfast, which is the meal at the end of the longest interval. Moreover, those who have endured long fasts testify that hunger may disappear completely after a period of two or three days, particularly if not much exercise is taken.

The function of hunger is to insure the taking of food. This is an act essential to life, but in the lower animals, and in children, is not recognized as such through the operation of associative memory, and, therefore, is not to be depended on to be performed volitionally. It is essentially a reflex act and hunger is the sensory basis for the reflex. As we shall learn in a later chapter, an important feature of proper eating is the maintenance of regular habits in regard to it. Hunger serves as a powerful aid to regularity, for it tends to come on at about the time we are in the habit of eating. Many people suffer rather severely if obliged to wait through the period of a usual meal, although the interval measured in hours may be no longer than others to which they are accustomed and which cause no discomfort.

Thirst. This sense, in its ordinary form, arises from dryness of the throat. Apparently there are receptors in that region which are stimulated by deficiency of moisture. The throat is moistened by the saliva which is swallowed at frequent intervals, and the sense of thirst thus kept in abeyance. There is a constant loss of water from the Body by means of the various channels of excretion, lungs, sweat glands, etc. When the resultant diminution in the water content of the tissues reaches a certain point the swallowing of saliva no longer prevents stimulation of the thirst receptors, and liquid from outside the Body must be taken if the thirst is to be relieved. The liquid need not necessarily be swallowed. Injections directly into the veins are effective in abolishing thirst sensations.

If, as the result of prolonged deprivation, the water content of the Body is seriously diminished, ordinary thirst gives way to much more pronounced and finally very painful sensations. From these there is no relief with the passage of time as there may be in case of hunger. The distress becomes more and more marked leading ultimately, it is said, to mental breakdown. It is interesting that loss of the sense of thirst through accident or disease is rarer than loss of any other sense. Only one or two cases are on record of individuals in whom thirst has been absent.

The Cutaneous Receptors. These occur over the entire Body, not uniformly distributed but scattered in fine dots over the surface. This punctiform arrangement can be demonstrated by exploring the skin with suitable fine instruments. Such a procedure shows that the different cutaneous senses occur in distinct spots which do not overlap, but which in most parts of the Body are so intermingled as to leave no area of any size devoid of any one of the senses. Sensory spots are much more numerous and more closely packed together in such regions as the hands and face which are liable to come in contact with foreign bodies, than they are in the better protected surfaces of the trunk and limbs. Four sorts of cutaneous sense spots are recognized: those of pain, touch, warmth, and cold. Pain spots are more numerous than any of the others; touch spots rank next in number, it being estimated that on the trunk and limbs there are a half million of them; cold spots are only half as numerous as touch spots; warmth spots are fewest of all, their number being estimated at thirty thousand for the entire Body.

Pain. When the skin is powerfully stimulated by heat, cold or pressure, or is inflamed, we get a sensation which we call *pain.* This is something quite different from the unpleasantness caused by a dazzling light or a musical discord or a disagreeable odor or taste. We recognize these as being still sight or sound or smell or taste sensations. Pain, however, is always recognized as a distinct sensation having its own modality. Its function seems to be wholly one of warning; only when something is amiss do we feel it. Since danger results from strong stimulation but not from feeble stimulation pain receptors are less irritable than other sorts; it is estimated that the sense of touch is one thousand times as delicate as the sense of pain. Harm may result from excessive

stimulation of any sort. Pain receptors, therefore, are irritable to all forms of energy except that of light.

Because pain results from any sort of stimulation, but only when excessive, it was formerly thought to be not a distinct sense but the result of overstimulation of the other senses. Direct evidence has accumulated, however, showing that pain is a distinct sense, with receptors and nerve tracts of its own. For one thing, there are regions of the Body, notably the dentine and pulp of the teeth and the tympanic membranes (ear-drums), in which stimulation gives rise to pain only, no other sensations being elicitable; conversely, the mucous membrane of certain areas of the cheeks contains receptors for touch, but no amount of stimulation will arouse sensations of pain. Furthermore, the afferent paths for pain in the spinal cord are distinct from those for some of the other body-senses, which could scarcely be true of pain were no more than the effect of overstimulation of receptors in general. If certain parts of the cord are cut in the thoracic region of a rabbit, gentle touches on the hind limb appear to be felt; the animal erects its ears or moves its head: but powerful stimulation of the sciatic nerve causes no signs of pain, while if the dorsal white columns be cut the animal can feel stimuli applied to the hind limb and sufficient to cause pain under normal conditions, but it appears insensible to gentle pressure on the skin. In human beings very similar phenomena have been observed in cases of spinal cord disease: and in a certain stage of chloroform or ether narcosis the patient feels the surgeon's hand or his knife where it touches the skin, but he experiences no pain when deeper parts are cut.

Pain receptors are very widely distributed over the skin and through most parts of the Body; in fact pain is believed to be the most widely distributed of the senses. Histological examination fails to reveal any special organs at the terminations of pain fibers in the skin or elsewhere, so that the idea has prevailed that pain results from direct stimulation of naked nerve endings. There is evidently, however, some sort of modification of these endings to fit them to serve as receptors, since they have a lower threshold for painful stimulation than do naked nerves elsewhere. It is noteworthy, nevertheless, that the sensations evoked by artificial stimulation of nerve trunks along their course, when the "funny bone" is hit, or when there is inflammation, as in neuralgia, are usually only of pain.

Pains can be localized, though only imperfectly, and the less perfectly the more severe they are. The exact place of a needle prick after removal of the needle (so that there is no guiding concomitant touch sensation) cannot be recognized as well as a pin touch on the same region of the skin, but still fairly well; while the acute pain caused by a small abscess (bone felon) under the periosteum of a finger bone is often felt all over the forearm; and a single diseased tooth may cause pain felt over the whole of that side of the face.

Many internal pains instead of being felt as coming from the organ where they originate are referred to areas of the skin. So constant is this misreference that the physician is able to judge of the seat of many disturbances from the particular skin areas that exhibit tenderness. The explanation of this misreference of internal pain to the skin is not easy to make. It has been suggested that the nerve-paths over which internal pains reach the body sense-area of the cortex lie close to those of pains from certain skin areas; and that since painful skin stimulation is much more common than internal pains, the brain interprets all impulses reaching it over a restricted nerve-path as coming from the particular skin area whose nerve-path forms part of the whole nerve-path in question.

Touch or the Pressure Sense. Through touch proper we recognize delicate pressure or traction exerted on the skin. Pure touch, *i. e.*, stimulation of pressure receptors only, is confined to pressures below about 10 gms. ($^1/_3$ oz.); above that figure muscle-sense receptors are always stimulated also; moreover, we rarely touch anything without at the same time getting temperature sensation; therefore pure tactile feelings are rare. In regions where hairs are present the touch receptors are located near the bases of hairs in such position that the hairs act as levers, transmitting pressures applied to them with increased force to the receptors at their roots; the delicacy of the sense is thus much increased. The vibrissæ (whiskers) of cats and other animals illustrate this extension of the pressure sense emphatically. It is interesting that seals and walruses may have vibrissæ nearly as large as an ordinary lead pencil. In nonhairy regions definite structures (Meissner's corpuscles) function as tactile receptors.

The delicacy of the pressure sense varies on different parts

of the skin; it is greatest on the forehead, temples, and back of the forearm, where a weight of 2 milligr. (0.03 grain) pressing on an area of 9 sq. millim. (0.0139 sq. inch) can be felt. On the front of the forearm 3 milligr. (0.036 grain) can be similarly felt, and on the front of the forefinger 5 to 15 milligr. (0.07–0.23 grain).

In order that the sense of touch may be excited neighboring skin areas must be differently pressed; when we lay the hand on a table this is secured by the inequalities of the skin, which prevent end organs, lying near together, from being equally compressed. When, however, the hand is immersed in a liquid, as mercury, which fits into all its inequalities and presses with practically the same weight on all neighboring immersed areas, the sense of pressure is only felt at a line along the surface, where the immersed and nonimmersed parts of the skin meet.

The Localizing Power of the Skin. When the eyes are closed and a point of the skin is touched we can with some accuracy indicate the region stimulated; although tactile feelings are in general characters alike, they differ in something (*local sign*) besides intensity by which we can distinguish them; some sensation quality must be present enabling us to tell from one another two precisely similar contacts of an external object when applied, say, to the tips of the fore and ring fingers respectively. The accuracy of the localizing power is not nearly so great as in the eye and varies widely in different skin regions; it may be measured by observing the least distance which must separate two objects (as the blunted points of a pair of compasses) in order that they may be felt as two. The following table illustrates some of the differences observed:

Tongue-tip	1.1 mm. (0.04 inch)
Palm side of last phalanx of finger	2.2 mm. (0.08 inch)
Red part of lips	4.4 mm. (0.16 inch)
Tip of nose	6.6 mm. (0.24 inch)
Back of second phalanx of finger	11.0 mm. (0.44 inch)
Heel	22.0 mm. (0.88 inch)
Back of hand	30.8 mm. (1.23 inches)
Forearm	39.6 mm. (1.58 inches)
Sternum	44.0 mm. (1.76 inches)
Back of neck	52.8 mm. (2.11 inches)
Middle of back	66.0 mm. (2.64 inches)

The fact brought out above, that the tip of the tongue has much greater localizing power than any other region, accounts for the apparently large size of small objects that become lodged between the teeth, and of small roughnesses on the latter. The localizing power is surprisingly small over most of the Body. It is a little more acute measured across a limb than parallel with its long axis; it is also improvable with practice, as evidenced in the superior tactile sensibility of the blind.

The obvious explanation that suggests itself for this localizing power is that it depends on nerve distribution; that each touch nerve has connection with a special cell or group of cells in the cerebral cortex whose excitation causes a sensation with a characteristic local sign; and at the peripheral end is distributed over a certain skin area; the larger the area the further apart must the stimuli be applied in order to be perceived as distinct. Two apparent difficulties with this explanation have been: first, that localizing power improves with practice; and second, that according to it the localizing power should be greater along the lines where two sensory areas adjoin than when measured from the middle of one area to the middle of another, which seems not to be the case; the fact being that the compass points must be placed about so far apart wherever applied on an area of given localizing power. By a slightly different method of experimentation, *i. e.*, by applying the two points a second apart instead of simultaneously, it has been shown that the localizing power does depend on nerve distribution, but that the individual sensory areas are smaller than formerly believed. The reason the localizing power is so dull in unpracticed regions is that in them one or more unstimulated sensory areas must intervene between stimulated areas in order for separate sensations to be felt *when the areas are stimulated simultaneously*. Thus we see why the back of a knife laid on the surface causes a continuous linear sensation, although it touches many distinct nerve areas; if we could discriminate the excitations of each of these from that of its immediate neighbors we would get the sensation of a series of points touching us, one for each nerve region excited; but in the absence of intervening unexcited nerve areas the sensations are fused together.

The Temperature Sense. By this we mean our faculty of perceiving cold and warmth; and, with the help of these sensations,

of perceiving temperature differences in external objects. As already stated the temperature receptors are of two sorts: the receptors for cold, which are near the surface of the skin and very numerous; and the receptors for warmth, which are about 0.1 mm. (1/250 in.) further below the surface, and are relatively much fewer.

To form a satisfactory picture of the working of these two kinds of receptors it is necessary to realize that under all ordinary circumstances the Body is considerably warmer than its surroundings (p. 574), so that there is normally a steady flow of heat from the Body to the outside through the skin. This heat-flow tends to keep the skin temperature somewhere near that of the inside of the Body, but it is clear that if the exterior cools off the skin is likely to cool off with it and vice versa. Thus changes in skin temperature go hand in hand to a certain extent with changes in external temperature. This parallelism may be disturbed, however, by changes in the blood-flow through the skin (p. 392). Whenever the skin is flushed by an abundant circulation of blood through it it tends to become warmer, and whenever it is pale, due to a decrease in circulation, it tends to become cooler.

We may say, in general, that whenever the temperature of the skin is not changing, and is not so extremely hot or cold as to excite pain receptors, the temperature receptors are quiescent, and we have no sensations of either warmth or cold. When the temperature of any portion of the skin is *rising*, warmth receptors are excited, giving us corresponding sensations. When the temperature of any portion of the skin is *falling*, cold receptors are excited, and we feel sensations of cold. It should be noted that these excitations occur whatever may be the actual temperature background against which they are aroused. Thus whether the skin is cool or warm a drop in temperature brings about sensations of cold, and a rise, sensations of warmth. This is well illustrated by the fact that one's hand nearly always feels cool to his cheek and warm to his ear. The usual temperature of the hand is intermediate between that of the cheek and of the ear; consequently when the hand is laid against both the latter regions at once it causes a fall of temperature in the former and a rise in the latter, with sensations as described.

Many of our temperature experiences can be explained in terms of the simple statement above, but not all. Thus we make a

definite distinction between warmth and "hotness." This distinction depends on the fact that when a rise in temperature occurs against a background temperature of more than 41° or 42° C. (108°–110° F.) the receptors for cold are excited along with those for warmth. The definite sensation of "hot" is due to this simultaneous excitation of the two sorts of receptors. When the temperatures become so extreme as to verge on pain, as when the feet are very cold or the hands are held in hot water, sensations of cold or hot may be felt when the temperature is not actually changing. Thus at these extremes the statement that excitation is due to a temperature change does not hold.

Temperature sensations may have either external or internal reference; in other words, we may think of objects in contact with the Body, or of the surrounding air or water, as being warm or cold, or we may think of the Body itself as being one or the other. In general sensations of warmth are perceived as bodily states only when the skin is flushed, and the sensations are due in part to warmth contributed by the blood. Similarly, for the Body or a portion of it to feel cold the skin must be pale, and the lowering of temperature dependent in part on the inadequacy of the blood-flow.

Although the temperature receptors have been spoken of as in the skin their distribution is actually somewhat wider; they are present also in the mucous membrane of the mouth and throat, the pharynx and upper part of the gullet, and the entry of the nostrils.

Place of Tactile Sensations in the Mental Life. From an evolutionary point of view the combined tactile sensations, touch, muscle-sense (when evoked by pressure), and temperature, are probably the earliest non-noxious sensations to have been distinctly differentiated, and this primary position they still largely hold in our mental life; we mainly think of the things about us as objects which would give us certain tactile sensations if we were in contact with them. Though the eye tells us much quicker, and at a greater range, what are the shapes of objects and whether they are smooth, rough, and so on, our real conceptions of round and square and rough bodies are derived through touch, and we largely translate unconsciously the teachings of the eye into mental terms of the tactile sense.

The Peripheral Reference of our Sensations. Repeated mention has been made of the fact that we refer our external sensations to the outside world; this is only one case of a more general law, in accordance with which we do not ascribe our sensations, as regards their locality, to the brain, where the sensation is actually aroused, but to a peripheral part. With respect to the brain, other parts of the Body are external objects as much as the rest of the material universe, yet we locate the majority of our internal sensations at the places where the sensory nerves concerned are irritated, and not in the brain. Even if a nerve-trunk be stimulated in the middle of its course, we refer the resulting sensation to its outer endings. A blow on the inside of the elbow-joint, injuring the ulnar nerve, produces not only a local pain, but a sense of tingling ascribed to the fingers to which the ends of the fibers go. Persons with amputated limbs have feelings in their fingers and toes long after they have been lost, if the nerve-trunks in the stump be irritated. This persistent reference is commonly ascribed to the results of experience. The events of life have taught us that in the great majority of instances the sensory impulses which excite a given tactile sensation, for example, have acted upon the tip of a finger. The sensation goes when the finger is removed, and returns when it is replaced; and the eye confirms the contact of the external object with the finger-tip when we get the tactile sensation in question. We thus come firmly to associate a particular region of the skin with a given sensation, and whenever afterwards the nerve-fibers coming from the finger are stimulated, no matter where in their course, we ascribe the origin of the sensation to something acting on the finger-tip.

Perceptions. In every sensation we have to distinguish carefully between the pure sensation and certain judgments founded upon it; we have to distinguish between what we really feel and what we think we feel; and very often firmly believe we do feel when we do not.

The most important of these judgments is that which leads us to ascribe certain sensations, those aroused through organs of special sense, to external objects—that outer reference of our sensations which leads us to form ideas concerning the existence, form, position, and properties of external things. Such representations as these, founded on our senses, are called *perceptions.*

Since these always imply some mental activity in addition to a mere feeling, their full discussion belongs to the domain of Psychology. Physiology, however, is concerned with them so far as it can determine the conditions of stimulation under which a given mental representation concerning a sensation is made. It is quite certain that we can feel nothing but states of ourselves, but, as already pointed out, we have no hesitation in saying we feel a hard or a cold, a rough or smooth body. When we look at a distant object we usually make no demur to saying that we perceive it. What we really feel is, however, the change produced by it in our eyes. There are no parts of our Bodies reaching to a tree or a house a mile off—and yet we seem to feel all the while that we are looking at the tree or the house and feeling them, and not merely experiencing modifications of our own eyes or brains. When reading we *feel* that what we really see is the book; and yet the existence of the book is a judgment founded on a state of our Body, which alone is what we truly feel.

We have the same experience in other cases, for example with regard to touch.

Hairs are quite insensible, but are imbedded in the sensitive skin, which is excited when they are moved. But if the tip of a hair be touched by some external object we believe we feel the contact at its insensible end, and not in the sensitive skin at its root. So, the hard parts of the teeth are insensible; yet when we rub them together we refer the seat of the sensation aroused to the points where they touch one another, and not to the sensitive parts around the sockets where the sensory nerve impulse is really started.

Still more, we may refer tactile sensations, not merely to the distal ends of insensible bodies implanted in the skin, but to the far ends of things which are not parts of our Bodies at all; for instance, the distant end of a rod held between the finger and a table while the finger is moved a little from side to side. We then believe we feel touch or pressure in two places; one where the rod touches our finger, and the other where it comes in contact with the table. A blind man gropes his way along by *feeling* at the end of his stick.

This irresistible mental tendency to refer certain of our states of feeling to causes outside of our Bodies, whether in contact with

them or separated from them by a certain space, is known as the phenomenon of the *extrinsic reference of our sensations*. It seems largely to depend on the fact that the sensations extrinsically referred can be modified by movements of our Bodies. Hunger, thirst, and toothache all remain the same whether we turn to the right or left, or move away from the place we are standing in. But a sound is altered. We may find that in a certain position of the head it is heard more by the right ear than the left; but on turning round the reverse is the case; and halfway round the loudness in each ear is the same. Hence we are led, by mental laws outside of the physiological domain, to suspect that its cause is not in our Body, but outside of it; and depends not on a condition of the Body but on something else.

Sensory Illusions. "I must believe my own eyes" and "we can't always believe our senses" are two expressions frequently heard, and each expressing a truth. No doubt a sensation in itself is an absolute incontrovertible fact: if I feel redness or hotness I do feel it, and that is an end of the matter: but if I go beyond the fact of my having a certain sensation and conclude from it as to properties of something else—if I form a *judgment* from my *sensation*—I may be totally wrong; and in so far be unable to believe my eyes or skin. Such judgments are almost inextricably woven up with many of our sensations, and so closely that we cannot readily separate the two; not even when we know that the judgment is erroneous.

For example, the moon when rising or setting appears bigger than when high in the heavens—we seem to feel directly that it arouses more sensation, and yet we know certainly that it does not. With a body of a given brightness the amount of change produced in the end organs of the eye will depend on the size of the image formed in the eye, provided the same part of its sensory surface is acted upon. Now the size of this image depends on the distance of the object; it is smaller the farther off it is and greater the nearer, and measurements show that the area of the sensitive surface affected by the image of the rising moon is no larger than that affected by it when overhead. Why then do we, even after we know this, see it bigger? The reason is that when the moon is near the horizon we imagine, unconsciously and irresistibly, that it is farther off; even astronomers who know perfectly well that

it is not, cannot help forming this unconscious and erroneous judgment—and to them the moon appears in consequence larger when near the horizon, just as it does to less well-informed mortals. In fact we have a conception of the sky over which the moon seems to travel, not as a half sphere but as somewhat flattened, and hence when the moon is at the horizon we unconsciously judge that it is farther off than when overhead. But any body which excites the same extent of the sensitive surface of the eye at a great distance that another does at less, must be larger than the latter; and so we conclude that the moon at the horizon is larger than the moon in the zenith, and are ready to declare that we see it so.

Erroneous perceptions of this sort are known as *sensory illusions;* and we ought to be constantly on guard against them.

CHAPTER XIV

THE EAR. HEARING AND EQUILIBRATION. TASTE AND SMELL

Functions of the Ear. The ear is not solely an organ of hearing. It includes, in addition, the highly important structures by which is mediated the sense of equilibrium. Hearing is, however, its familiar function, and we will consider it first in order. To be able to discuss intelligently the apparatus for hearing we must have in mind the fundamental facts about the agency by which the sense is aroused, namely, *sound.*

The Loudness, Pitch, and Timbre of Sounds. Sounds, as sensations, fall into two groups—*notes* and *noises.* Physically, sounds consist of vibrations, and these, under most circumstances, when they first reach our auditory organs, are alternating rarefactions and condensations of the air, or *aërial waves.* When the waves follow one another uniformly, or *periodically,* the resulting sensation (if any) is a note; when the vibrations are irregular it is a noise. In notes we recognize (1) loudness or intensity; (2) pitch; (3) quality or *timbre,* or, as it has been called, *tone color;* a note of a given loudness and pitch produced by a flute and by a violin has a different character or individuality in each case; this quality is its *timbre.* In order to understand the working of the auditory mechanism we must get some idea of the physical qualities in objective sound of which the subjective differences of auditory sensations are signs.

The *loudness* of a sound depends on the force of the aërial waves; the greater the intensity of the alternating condensations and rarefactions of these, the louder the sound. The *pitch* of a note depends on the length of the waves, that is, the distance from one point of greatest condensation to the next, or (what amounts to the same thing) on the number of waves reaching the ear in given time, say a second. The shorter the waves the more rapidly they follow one another, and the higher the pitch of the note. When audible vibrations bear the ratio 1:2 to one another, we hear the musical

interval called an octave. The middle *C* of the musical scale is due to 256 vibrations per second. Its octave has 512 vibrations.

Sound vibrations may be too rapid or too slow in succession to produce sonorous sensations. The highest-pitched audible note answers to about 20,000 vibrations in a second, but it differs in individuals; many persons cannot hear the cry of a bat nor the chirp of a cricket, which lie near this upper audible limit. On the other hand, sounds of vibrational rate about 40 per second are not well heard, and a little below this become inaudible. The highest note used in orchestras is the d^v of the fifth accented octave, produced by the piccolo flute, due to 4,752 vibrations in a second; and the lowest-pitched is the E_1, of the contra octave, produced by the double bass. Modern grand pianos and organs go down to *C*, in the contra octave (33 vibrations per second) or even *A*″, (27½), but the musical quality of such notes is imperfect; they produce rather a "hum" than a true tone sensation, and are only used along with notes of higher octaves to which they give a character of greater depth.

Timbre. Since the loudness of a tone depends on the vibrational amplitude of its physical antecedent, and its pitch on the vibrational rate, we have still to seek the cause of *timbre;* the quality by which we recognize the human voice, the violin, the piano, and the flute, even when all sound the same note and of the same loudness. Helmholtz showed that the quality of any tone is determined by the particular *overtones* or *harmonic partials* that are combined in it with the fundamental tone. Most vibrating bodies are able to vibrate both as a whole and in sections. Since the sections are smaller than the whole body their vibrations are more rapid than those of the body as a whole. The vibrating sections may be halves, thirds, fourths, or any other fraction of the whole body. Also one and the same body may be vibrating at once in halves, quarters, and several other smaller divisions. These vibrations in parts are the sources of *overtones,* the *pitch* of the tone being determined by its vibration as a whole, the so-called *fundamental* vibration.

The air waves set in motion by a body vibrating in such complex fashion must necessarily be themselves very complex. Since they are periodic, however, they produce audible notes, if rapid and intense enough. The actual form of air wave which proceeds

from a body vibrating thus depends upon the particular components which make it, and it has been shown that any complex periodic vibration can be analyzed mathematically into its constituents, and these unerringly determined. The timbre of a tone depends, then, according to our former definition, upon the form of air wave which enters the ear. A tone composed of a fundamental and three overtones will come to the ear as a wave having quite a different form from one having in addition to the fundamental five partials.

Whereas we ordinarily hear compound tones merely as tones of certain quality, the trained ear is able to hear and pick out the overtones by which the quality is determined. It is evident, therefore, that the ear is able to analyze compound tones into their individual constituents.

Sympathetic Resonance. Imagine slight taps to be given to a pendulum; if these be repeated at such intervals of time as always to help the swing and never to retard it, the pendulum will soon be set in powerful movement. If the taps are irregular, or when regular come at such intervals as sometimes to promote and sometimes retard the movement, no great swing will be produced; but if they always push the pendulum in the way it is going at that instant, they need not come every swing in order to set up a powerful vibration; once in two, three, or four swings will do. A stretched string, such as that of a piano, is so far like a pendulum that it tends to vibrate at one rate and no other; if aërial waves hit it at exactly the right times they soon set it in sufficiently powerful vibrations to cause it to emit an audible note. By using such strings we can analyze compound tones and thus prove objectively that they are made up of partials. If the dampers of a piano be raised and a note be sung loudly to it, it will be found that several strings are set in vibration, such vibrations being called *sympathetic*. The human voice emits compound tones which can be mathematically analyzed into simple vibrations, and if the piano strings set in movement by it be examined, they will be found to be exactly those which answer to these vibrations and to no others. We thus get experimental grounds for believing that compound tones are really made up of a number of simple vibrations, and get an additional justification for the supposition that in the ear each note is analyzed into its components; and that the difference

of sensation which we call timbre is due to the effect of the secondary partial tones thus perceived.

The External Ear. The auditory organ in man consists of three portions, known respectively as the *external ear*, the *middle ear* or *tympanic cavity*, and the *internal ear* or *labyrinth;* the latter contains the end organs of the auditory nerve. The external ear consists of the expansion seen on the exterior of the head, called the *concha*, *M*, Fig. 68, and a passage leading in from it, the *external auditory meatus*, *G*. This passage is closed at its inner end

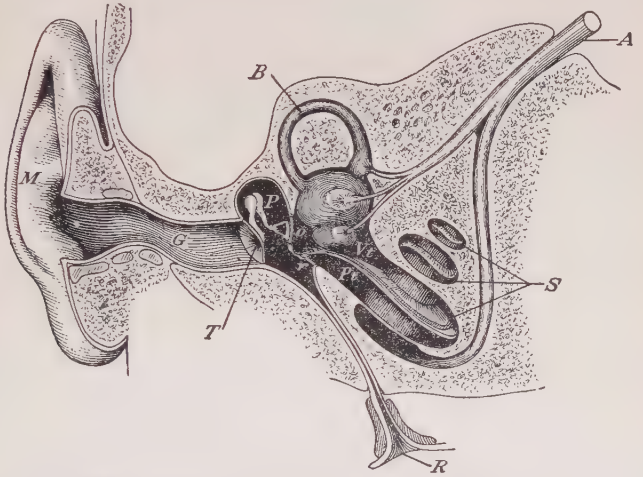


Fig. 68.—Semidiagrammatic section through the right ear (Czermak). *M*, concha; *G*, external auditory meatus; *T*, tympanic membrane; *P*, middle ear; *o*, oval foramen; *r*, round foramen; *R*, pharyngeal opening of Eustachian tube; *V*, vestibule; *B*, a semicircular canal; *S*, the cochlea; *Vt*, scala vestibuli; *Pt*, scala tympani; *A*, auditory nerve.

by the *tympanic* or *drum membrane*, *T*. It is lined by skin, through which numerous small glands, secreting the *wax* of the ear, open.

The Functions of the Tympanic Membrane. If a stretched membrane, such as a drumhead, be struck, it will be thrown into periodic vibration and emit for a time a note of a determined pitch. The smaller the membrane and the tighter it is stretched the higher the pitch of its note; every stretched membrane thus has a rate of its own at which it tends to vibrate, just as a piano or violin string has. When a note is sounded in the air near such a membrane, the alternating waves of aërial condensation and rarefaction will move

it; and if the waves succeed at the vibrational rate of the membrane the latter will be set in powerful *sympathetic vibration;* if they do not push the membrane at the proper times, their effects will neutralize one another: hence such membranes respond well to only one note. The tympanic membrane, however, responds equally well to a large number of notes; at least for those due to aërial vibrations of rates from 60 to 4,000 per second, running over eight octaves and constituting those commonly used in music. This faculty depends on two things: (1) the membrane is comparatively loosely and not uniformly stretched; (2) it is *loaded* by the tympanic bones.

The drum-membrane is a shallow funnel with its point toward the middle ear and its sides convex towards the external auditory meatus; something like an umbrella turned inside out; in such a membrane the tension is not uniform but increases towards the center, and it has accordingly no proper note of its own. Further, whatever tendency such a membrane may have to vibrate rather at one rate than another, is almost completely removed by "damping" it, *i. e.*, placing in contact with it something comparatively heavy and which has to be moved when the membrane vibrates. This is effected by the tympanic bones, fixed to the drum-membrane by the handle of the malleus. Another advantage is gained by the damping; once a stretched membrane is set vibrating it continues so doing for some time; but if loaded its movements cease almost as soon as the moving impulses. The dampers of a piano are for this purpose; and violin-players have to "damp" with the fingers the strings they have used when they wish the note to cease. The tympanic bones act as dampers.

The Middle Ear (*P*, Fig. 68) is an irregular cavity in the temporal bone, closed externally by the drum membrane. From its inner side the *Eustachian tube* (*R*) proceeds to the pharynx, and the mucous membrane of that cavity is continued up the tube to line the middle ear; the proper tympanic membrane composed of connective tissue is therefore covered by mucous membrane on its inner, as it is by very thin skin on its outer, side. In the bony inner wall of the middle ear are two small apertures, the *oval* and *round foramens*, *o* and *r*, which lead into the labyrinth. During life the round aperture is closed by the lining mucous membrane, and the oval in another way, to be described presently. The

tympanic membrane, *T*, stretched across the outer side of the middle ear, forms a shallow funnel as stated above. It is pressed by the external air on its exterior, and by air entering the tympanic cavity through the Eustachian tube on its inner side. If the middle ear were permanently closed it could contain no air, but only such gas as might enter it from the blood. The result would be that the pressures on the inner and outer sides of the drum membrane would not be always equal when barometric pressure varied, and the membrane would be bulged in or out according as the external or internal pressure on it were the greater. This unequal pressure would interfere seriously with the freedom of vibration of the membrane and so impair hearing. On the other hand, were the Eustachian tube always open the sounds of our own voice would be loud and disconcerting, so it is usually closed; but every time we swallow it is opened, and thus the air-pressure in the cavity is kept equal to that in the external auditory meatus. By holding the nose, keeping the mouth shut, and forcibly expiring, air may be forced under pressure into the middle ear, and will be held in part imprisoned there until the next act of swallowing. On making a balloon ascent or going rapidly down a deep mine, the sudden and great change of aërial pressure outside frequently causes painful tension of the drum membrane, which may be greatly alleviated by frequent swallowing movements.

The great importance of the Eustachian tubes in hearing is illustrated by the deafness that results from their continued closure. This condition is frequently brought about in children by the growth of adenoids (see p. 404) in the back of the throat, which press upon and close the Eustachian tubes.

Essential as these tubes are for good hearing they constitute a frequent source of ear trouble. The congestion of the mucous membranes of the throat and nose in a "cold in the head" is apt to involve the Eustachian tubes and the lining of the middle ear. Sometimes an exudate from the congested membranes fills the middle ear completely, and by its pressure causes acute pain, as well as deafness. Unless relief is obtained the tympanic membrane may be ruptured. Earache resulting from a cold should therefore not be neglected. Less commonly but more seriously, actual infection (p. 322) of the middle ear may occur, the infection invading the region by way of the Eustachian tubes. The mastoid process

(the prominent bony mass just behind the ear) has many hollows in it which communicate with the cavity of the middle ear and may become infected from it. Infection of these hollows gives rise to the extremely grave condition, *mastoiditis.*

The Auditory Ossicles. Three small bones lie in the middle ear forming a chain from the drum membrane to the oval foramen. The external bone (Fig. 69) is the *malleus* or *hammer;* the middle one, the *incus* or *anvil;* and the internal, the *stapes* or *stirrup.* The malleus, *M*, has an upper enlargement or *head,* which carries on its inner side an articular surface for the incus; below the head is a constriction, the *neck,* and below this two processes complete the bone; one, the *long* or *slender process,* is imbedded in a ligament which reaches from it to the front wall of the tympanic cavity; the other process, the *handle,* reaches down between the mucous membrane lining the inside of the drum membrane and the membrane proper, and is firmly attached to the latter near its center and keeps the membrane dragged in there so as to give it its peculiar concave form, as seen from the outside. The incus has a body and two processes, and is much like a molar tooth with two roots. On its body is an articular hollow to receive the head of the malleus; its short process (*Jb*) is attached by ligament to the back wall of the tympanum; the long process (*Jl*) is directed inwards to the stapes; on the tip of this process is a little knob, which represents a bone (*os orbiculare*) distinct in early life. The stapes (*S*) is extremely like a stirrup, and its base (the footpiece of the stirrup) fits into the oval foramen, to the margin of which its edge is united by a fibrous membrane, allowing of a little play in and out.

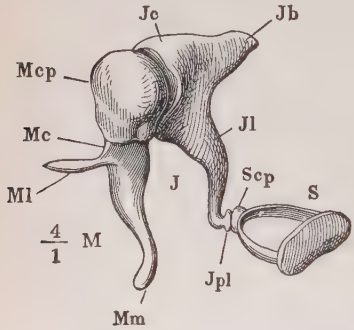


FIG. 69.—The auditory ossicles of the right ear, seen from the front. M, malleus; *J*, incus; *S*, stapes; *Mcp*, head of the malleus; *Mc*, neck of ditto; *Ml*, long process; *Mm*, handle; *Jc*, body; *Jb*, short, and *Jl*, long process of incus; *Jpl*, *os orbiculare;* *Scp*, head of stapes.

From the posterior side of the neck of the malleus a ligament passes to the back wall of the middle ear: this, with the ligament imbedding the slender process and fixed to the front wall of the cavity, forms an anteroposterior *axial ligament,* on which the

malleus can rotate slightly, so that the handle can be pushed in and the head out and *vice versa*. If a pin be driven through Fig. 69 just below the neck of the malleus and perpendicular to the paper it will very fairly represent this axis of rotation. Connected with the malleus is a tiny muscle, called the *tensor tympani;* it is inserted on the handle of the bone below the axis of rotation, and when it contracts pulls the handle in and tightens the drum membrane. Another muscle (the *stapedius*) is inserted into the outer end of the stapes, and when it contracts fixes the bone so as to limit its range of movement in and out of the oval window.

Functions of the Auditory Ossicles. When the air in the external auditory meatus is condensed it pushes in the tympanic membrane which carries with it the handle of the malleus. This bone then slightly rotates on the axial ligament and, locking into the incus where the two bones articulate, causes the long process (*Jl*, Fig. 69) of the latter to move inwards. The incus thus pushes in the stapes; the reverse occurs when air in the auditory passage is rarefied. Aërial vibrations thus set the chain of bones swinging, and push in and pull out the base of the stapes, which sets up waves in the fluid of the labyrinth. This fluid being chiefly water, and practically incompressible, the end of the stapes could not work in and out at the oval foramen, were the labyrinth elsewhere completely surrounded by bone: but the membrane covering the round foramen bulges out when the base of the stapes is pushed in, and *vice versa;* and so allows of waves being set up in the labyrinthic fluid. These correspond in period and form to those in the auditory meatus; their amplitude is determined by the extent of the vibrations of the drum membrane.

The form of the tympanic membrane causes it to transmit to its center, where the malleus is attached, vibrations of its lateral parts in diminished amplitude but increased power; so that the tympanic bones are pushed only a little way but with considerable force. Its area, too, is about twenty times as great as that of the oval foramen, so that force collected on the large area is, by pushing the tympanic bones, all concentrated on the smaller. The ossicles also form a bent lever (Fig. 69) of which the fulcrum is at the axial ligament and the effective outer arm of this lever is about half as long again as the inner, and so the movements transmitted by the drum membrane to the handle of the malleus are com-

municated with diminished range, but increased power, to the base of the stapes.

Ordinarily sound-waves reach the labyrinth through the tympanum, but they may also be transmitted through the bones of the head; if the handle of a vibrating tuning-fork be placed on the top of the head, the sounds heard by the person experimented upon seem to have their origin inside his own cranium. Similarly when a vibrating body is held between the teeth, sound reaches the end organs of the auditory nerve through the skull-bones; and persons who are deaf from disease or injury of the tympanum can thus be made to hear. Of course if deafness be due to disease of the proper nervous auditory apparatus no device can make the person hear.

The Internal Ear. The labyrinth consists primarily of chambers and tubes hollowed out in the temporal bone and inclosed by it on all sides, except for the oval and round foramina on its exterior, and certain apertures on its inner side by which blood vessels and branches of the acoustic n rve enter; during life all these are closed water-tight in one way or another. Lying in the *bony labyrinth* thus constituted, are membranous parts, of the same general form but smaller, so that between the two a space is left; this is filled with a watery fluid, called the *perilymph;* and the *membranous internal ear* is filled by a similar liquid, the *endolymph.*

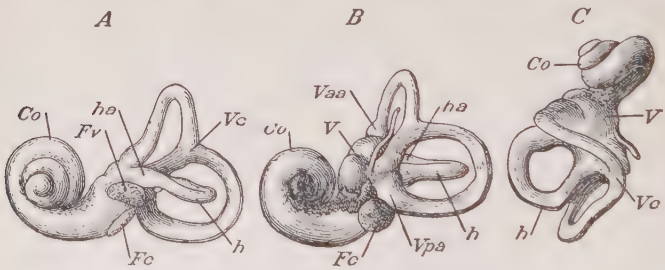


FIG. 70.—Casts of the bony labyrinth. *A*, left labyrinth seen from the outer side; *B*, right labyrinth from the inner side; *C*, left labyrinth from above; *Fc*, round foramen; *Fv*, oval foramen; *h*, horizontal semicircular canal; *ha*, its ampulla; *Vaa*, ampulla of anterior vertical semicircular canal; *Vpa*, ampulla of posterior vertical semicircular canal; *Vc*, conjoined portion of the two vertical canals.

The Bony Labyrinth. The bony labyrinth is described in three portions, the *vestibule*, the *semicircular canals*, and the *cochlea;* casts of its interior are represented from different aspects in Fig. 70. The vestibule is the central part and has on its exterior the oval

foramen (*Fv*) into which the base of the stirrup-bone fits. Behind the vestibule are three bony semicircular canals, communicating with the back of the vestibule at each end, and dilated near one end to form an *ampulla* (*Vpa*, *Vaa*, and *ha*). The horizontal canal lies in the plane which its name implies, and has its ampulla at the front end. The two other canals lie vertically, at right angles with each other, and at an angle of about 45°, to the median anteroposterior vertical plane of the head. Their ampullary ends are turned forwards and open close together into the vestibule; their posterior ends unite (*Vc*) and have a common vestibular opening.

The bony cochlea is a tube coiled on itself somewhat like a snail's shell, and lying in front of the vestibule.

The Membranous Labyrinth. The membranous vestibule, lying in the bony one, consist of two sacs communicating by a narrow aperture. The posterior is called the *utriculus*, and into it the membranous semicircular canals open. The anterior, called the *sacculus*, communicates by a tube with the membranous cochlea. The membranous semicircular canals much resemble the bony, and each has an ampulla; in most of their extent they are only united by a few irregular connective-tissue bands with the periosteum lining the bony canals; but in the ampulla one side of the membranous tube is closely adherent to its bony protector; at this point nerves enter the former. The relations of the membranous to the bony cochlea are more complicated. A section through this part of the auditory apparatus (Fig. 71) shows that its osseous portion consists of a tube wound two and a half times (from left to right in the right ear and *vice versa*) around a central bony axis, the *modiolus*. From the axis a shelf, the *lamina spiralis*, projects and partially subdivides the tube, extending farthest across in its lower coils. Attached to the outer edge of this bony plate is the membranous cochlea (*scala media*), a tube triangular in cross-section and attached by its base to the outer side of the

FIG. 71.—A section through the cochlea in the line of its axis.

bony cochlear spiral. The spiral lamina and the membranous cochlea thus subdivide the cavity of the bony tube (Fig. 72) into an upper portion, the *scala vestibuli*, *SV*, and a lower, the *scala tympani*, *ST*. Between these lie the lamina spiralis (*lso*) and the membranous cochlea (*CC*), the latter being bounded above by the membrane of Reissner (*R*) and below by the basilar membrane (*b*). The free edge of the lamina spiralis is thickened and covered with connective tissue which is hollowed out so as to form a spiral groove (the *sulcus spiralis*, *ss*) along the whole length of the membranous cochlea. The latter does not extend to the tip of the bony cochlea; above its apex the scala vestibuli and scala tympani join;

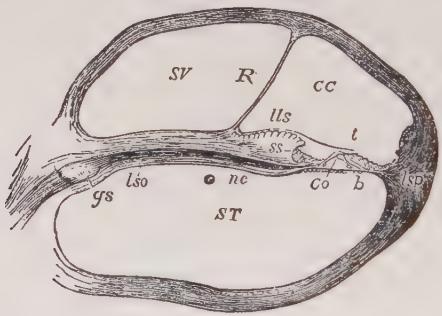


Fig. 72.—Section of one coil of the cochlea, magnified. *SV*, *scala vestibuli*; *R*, membrane of Reissner; *CC*, membranous cochlea (*scala media*); *lls*, *limbus laminæ spiralis*; *t*, tectorial membrane; *ST*, *scala tympani*; *lso*, spiral lamina; *Co*, rods of Corti; *b*, basilar membrane.

both are filled with perilymph, and the former communicates below with the perilymph cavity of the vestibule, while the scala tympani abuts below on the round foramen, which, as has already been pointed out, is closed by a membrane. The membranous cochlea contains certain solid structures seated on the basilar membrane and forming the *organ of Corti*; the rest of its cavity is filled with endolymph, which has free passage to that in the sacculus.

The Organ of Corti. This contains the end organs of the cochlear nerves. Lining the sulcus spiralis are cuboidal cells; on the inner margin of the basilar membrane the cells become columnar, and then are succeeded by a row which bear on their upper ends a set of short stiff hairs, and constitute the *inner hair-cells*, which are fixed below by a narrow apex to the basilar membrane; nerve-fibers

form direct contact with them. To the inner hair-cells succeed the *rods of Corti* (*Co*, Fig. 72), which are represented much magnified in Fig. 73. These rods are stiff and arranged side by side in two rows, leaned against one another by their upper ends so as to cover in a tunnel; they are known respectively as the *inner* and *outer rods*, the former being nearer the *lamina spiralis*. Each has a somewhat dilated base, firmly fixed to the basilar membrane; an expanded head where it meets its fellow; and a slender shaft uniting the two, slightly curved like an italic *f*. The inner rods are more slender and more numerous than the outer, the numbers being about 6,000 and 4,000 respectively. Attached to the external

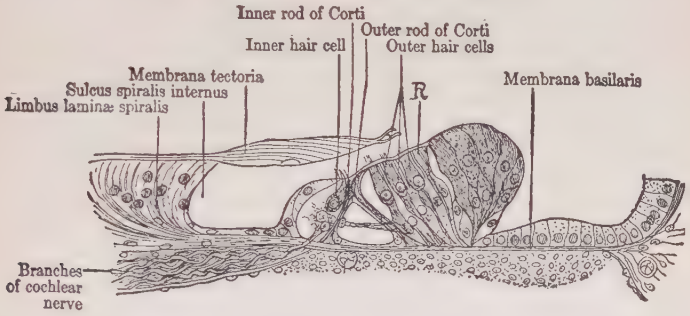


FIG. 73.—Section across the organ of Corti. *R*, reticular membrane; the other structures are named on the figure (Retzius, from Herrick's *Introduction to Neurology*).

sides of the head of the outer rods is the *reticular membrane* (*R*, Fig. 73), which is stiff and perforated by holes. External to the outer rods come four rows of *outer hair-cells*, connected like the inner row with nerve-fibers; their bristles project into the holes of the reticular membrane. Beyond the outer hair-cells is ordinary columnar epithelium, which passes gradually into cuboidal cells lining most of the membranous cochlea. The upper lip of the sulcus spiralis is uncovered by epithelium, and is known as the *limbus laminæ spiralis;* from it projects the *tectorial membrane* (*t*, Fig. 72) which extends over the rods of Corti and the hair-cells.

Function of the Cochlea. There is no doubt that the cochlea is the actual receptor for hearing in the sense that the translation of auditory vibrations into nerve impulses takes place within it. The problem confronting it is an exceedingly complex one, and at

present we are largely in the dark as to how it is met. According to various estimates that have been made, from six thousand to eleven thousand different tones, *i. e.*, distinct vibration rates; can be distinguished in the whole range of the ear. In other words, at least that many different nerve fibers must be available to receive and carry auditory impulses, and some machinery must exist whereby particular vibration rates excite definite fibers. The number of nerve-fibers (estimated at 14,000–16,000) is great enough; and since each ends in a single hair-cell the number of hair-cells is also enough; but from the way in which the hair-cells are mounted in relation to the rods of Corti it is difficult to see how single cells are picked out for stimulation by vibrations of any surrounding objects. The theories of hearing that are receiving most attention at present suppose the vibrations set up in perilymph and endolymph by the vibrations of the stapes in the oval foramen to be transmitted either to the basilar membrane, on which the organ of Corti rests, or to the tectorial membrane, which overlies the hair-cells, and appears to be in contact with the tips of the projecting hairs. Both membranes are wider at the apex of the cochlea than at its base (the less width of the lamina spiralis at the apex more than compensating for the less size of the bony tube there); both also vary in thickness in different parts. The assumption is that special areas of one or the other membrane respond particularly well to certain vibration rates; the vibrations of these special areas are supposed to be transmitted in turn to neighboring hair-cells and to bring about changes in the latter by which nerve impulses are set up. The picture is obviously very sketchy, but does not, so far as known, violate any physical laws nor assign to any cochlear structures functions they cannot possibly have.

We must suppose that compound tones entering the ear set the fluids of the cochlea into vibrations whose form depends on the make-up of the tones producing them. These vibrations of complex pattern presumably set the receptive membrane, whichever it is, into a series of vibrations at various levels, and so stimulate various hair-cells; the levels depending on the vibration rates of the fundamental and the partials of which the initial tone is composed. The membrane thus acts as an analyzer. The streams of nervous impulses entering the brain are again organized more or less completely into a unified sensation of certain quality.

Auditory Perceptions. Sounds, as a general rule, do not seem to us to originate within the auditory apparatus; we refer them to an external source, and to a certain extent can judge the *distance* and *direction* of this. As already mentioned, the extrinsic reference of sounds which reach the labyrinth through the general skull-bones instead of through the tympanic chain is imperfect or absent. The recognition of the distance of a sounding body is possible only when the sound is well known, and then not very accurately; from its faintness or loudness we may make in some cases a pretty good guess. Judgments as to the direction of a sound are based in animals, like horses, with movable external ears on muscle-sense perceptions of the direction in which the ears are pointed when the sound is best heard. In man, with his rudimentary and practically fixed external ears, this accurate means is not available; such judgments as to direction as he can form depend on the relative perception of intensity in the two ears (also in part on the relative vibration-phases). When the sound is perceived to be equal in both ears we judge it to be coming from some point in the mid-plane of the head, although whether from in front, above, or behind cannot be told until the head is moved; one of the most amusing and surprising experiments in sense perception is that in which this fact is demonstrated. It should be noted that equality of *sense perception* is stressed; this is because most persons differ in the acuteness of hearing in the two ears, and compensate unconsciously for the difference to just the extent necessary so that sounds that are actually of equal intensity are perceived as equal, in spite of the fact that the effect in one ear is really more pronounced than in the other. In judging the direction of sounds outside the mid-plane the same compensation is made when necessary. By turning the head and noting the accompanying changes of sensation in each ear we can localize sounds better than when the head is kept motionless. That the recognition of the direction of sounds is not a true sensation, but a judgment, founded on experience, is illustrated by the fact that we can estimate much more accurately the direction of the human voice, which we hear and heed most, than that of any other sound.

Nerve-Endings in the Semicircular Canals and the Vestibule. Myelinated fibers (*f*, Fig. 74) from the vestibular branch of the acoustic nerve are distributed along a line across the ampulla of

each semicircular canal. They lose their myelin sheath close to the basement membrane, *a*, which the dendrons pierce. The dendrons branch among the epithelium cells, which at this place are several rows thick, but appear to make connection only with the hair-cells.

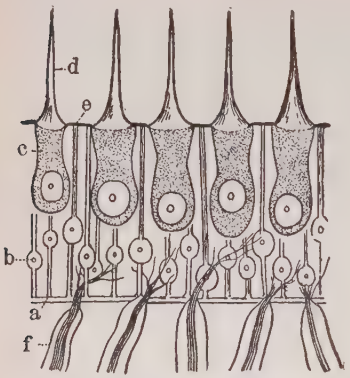


FIG. 74.—Diagram of epithelium in nervous region of ampulla of a semicircular canal.

The cells of the epithelium are of two varieties. The *columnar cells or hair-cells, c,* do not reach the basement membrane, and are nucleated or slightly granular: from the free end of each projects a rigid hair process, *d*. The remaining cells, *rod-cells, b,* are in several rows: each has a slender inner process extending to the basement membrane and an outer which reaches to the bases of the columnar cells and appears there to end in a rigid membrane, *e*, which is perforated for the passage of the hairs. They probably are mere supporting structures.

In some parts of the utricle and saccule are regions of epithelium very similar to that above described, and also supplied with nerve-fibers. In connection with them are found minute calcareous particles,—*otoliths* or ear-stones.

The Equilibrium Sense. An important group of proprio-ceptive impulses concerned primarily with the maintenance of bodily equilibrium and probably also with the maintenance of skeletal muscle tonus, is derived through the semicircular canals and vestibule of the ear, which are supplied by the vestibular portion of the acoustic nerve.

Experiment shows that cutting a semicircular canal is followed by violent movements of the head in the plane of the canal divided; the animal staggers, also, if made to walk; and, if a pigeon and thrown into the air, cannot fly. All its muscles can contract as before, but they are no longer so co-ordinated as to enable the animal to maintain or regain a position of equilibrium. It is like a creature suffering from giddiness; and similar phenomena follow, in man, electrical stimulation of the regions of the skull in which the semicircular canals lie.

If, moreover, a person lie perfectly quiet with closed eyes on a table which can be rotated, he is able to tell when the table is turned and in which direction, and often with considerable accuracy through what angle. If the rotation be continued for a time the feeling of it is lost, and then when the movement ceases there is a sense of rotation in the opposite direction. In such case, if the experiment has been made with sufficient care, neither tactile, muscular, nor visual sensations can help, and in the semicircular canals we seem to have a mechanism through which rotation of the head can give origin to afferent impulses, whether the head be passively moved with the rest of the Body or independently by its own muscles. Pressure of endolymph upon the cells lining the ampullæ, perhaps accentuated by the hairs projecting into the cavities, suggests itself as a means by which head movements in different planes may be translated into nerve impulses for mediating reflexes looking toward maintaining equilibrium, or regaining it when lost. It is important to bear in mind that this mechanism functions in connection with practically all our postural and locomotor reflexes, in other words, during much of our waking life, and in so doing arouses no conscious sensations. Its chief central connections are with the cerebellum, a fact which gives color to the view that it co-operates with muscle-sense in maintaining tonus (p. 202). But it also has connections with other regions of the brain, as evidenced by its action in maintaining equilibrium, and even with the cerebrum, as the conscious sensations referred to above show.

Supplementary to the semicircular canals are the structures of the vestibule, the utricle and saccule. These are hollow structures having stiff hairs projecting into their cavities and tiny otoliths caught among the hairs. The weight of the otoliths will affect the hairs among which it rests in one way when the head is erect, in quite another way when the head is horizontal. Thus the nerves may be stimulated differently for different positions of the head, fulfilling the conditions that the equilibrium sense requires. In many invertebrate animals structures similar to the utricle and saccule represent their only organs resembling our ears in any way. Experiments upon these animals have shown that in them these structures are not hearing organs but organs of equilibrium.

The equilibrium sense as a whole functions in two ways: to give

information as to the position of the head in space, so-called *static* equilibrium; and to give information concerning head movements, their direction and intensity, the latter constituting *dynamic* equilibrium. For every position of the head a particular sort of nerve-impulse stream is set up, and for every head-movement an impulse stream, characteristic of it, is aroused. It has been thought that the vestibule proper (utricle and saccule) is more concerned with static and the semicircular canals with dynamic equilibrium, but recent studies have shown that the organ as a whole functions to mediate both phases of the sense. A familiar example of the static phase is seen in the fact that a swimmer immersed in water knows perfectly whether he is on his face or back; whether his head is up or down, even though none of his other senses are contributing information concerning his position. Stimulation of the equilibrium receptors by motion of the head (the dynamic phase) results primarily in so-called *compensatory* movements. These are reflex movements either of the eyes or of the whole head. They can be demonstrated simply by holding a live frog, pigeon or small mammal firmly in the hand, with the head free, and turning it from side to side, watching the head meanwhile. It will be seen that the head moves in the opposite direction, and will do so with the eyes bandaged as well as with them open. Compensatory movements of the eyes can be seen in a person if they are watched carefully while he shakes his head vigorously from side to side.

Very pronounced or unusual stimulation of the equilibrium organs brings on reflex motions which may be described as compensatory movements carried to excess. Commonest of these are the jerking movements of the eyes (*nystagmus*) seen when a person who has been turning round and round comes to rest. Sensations of giddiness accompany nystagmus; these are probably aroused by impulses from receptors excited by the jerking movements of the eyes, although impulses from the equilibrium receptors may contribute in part. The nystagmus continues for some time after the stimulation of the equilibrium organ ceases. This was formerly supposed to mean that the prolonged rotation of the head to which the effect is due sets the endolymph in the canals into a whirling motion that continues after the head itself comes to rest. The cavities of the canals are so minute, however, as to make it improbable that any considerable motion of the

endolymph in them occurs, and practically certain that any motion that is set up ceases almost at once when the causative force subsides. We are therefore inclined to look on nystagmus as a "self-sustaining" reflex, *i. e.*, one in which afferent impulses from the jerking eyes suffice to keep them in reflex activity until fatigue sets in to interrupt the action. The pronounced effect of *unusual stimulation* is well illustrated by a common trick; persuade some one to place his forehead on the handle of an umbrella, the other end of which is on the floor, and then walk three or four times around it, rise, and try to go out of a door; he will nearly always fall; an unaccustomed pair of canals have been subjected to rotation with marked disaster to the equilibrium-maintaining function.

Taste. The organ of taste is the mucous membrane on the dorsum of the tongue* and, in some persons, of the soft palate and fauces. The nerves concerned are the glossopharyngeals, distributed over the hind part of the tongue, and the *lingual branches* of the inferior maxillary division of the trigeminals on its anterior two-thirds. It has been shown that the nerves of taste which reach the tongue by way of the trigeminal nerve spring from the medulla as part of the sensory branch of the facial.

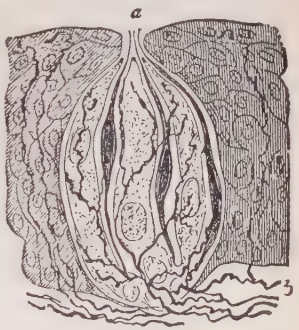


FIG. 75.—Taste-bud from a circumvallate papilla of the tongue: *a*, taste-pore; *b*, taste nerve-fibers (Merkle-Henle, from Herrick's *Introductoon to Neurology*).

On the tongue most of the sensory nerves run to papillæ; the circumvallate have the richest supply, and on these are peculiar end organs (Fig. 75) known as *taste-buds;* they are oval and imbedded in the epidermis covering the side of the papilla. Each consists, externally, of a number of flat, fusiform, nucleated cells and, internally, of six or eight so-called *taste-cells.* The latter are connected with nerve-fibers at their deeper ends. The capsule formed by the enveloping cells has a small opening on the surface; each taste-cell terminates in a very fine thread which there protrudes. Taste-buds are also found on some of the fungiform papillæ, and it is possible that simpler structures, not yet recognized, and consisting of single taste-cells are widely spread over the

* A description of the tongue will be found on p. 472.

tongue, since the sense of taste exists where no taste-buds can be found. The filiform papillæ are probably tactile.

In order for substances to be tasted they must be in solution: wipe the tongue dry and put a crystal of sugar on it; no taste will be felt until exuding moisture has dissolved some of the crystal. Excluding the burning sensations aroused by acid substances, tastes proper may be divided into sweet, bitter, acid, and saline. To some extent these taste perceptions are localized on the tongue. Most persons taste bitter things better with the back part of the tongue and sweet things with the tip, and in some persons the separation of function is quite complete. Chemical compounds are known which in such persons cause a pure sweet sensation if placed on the tongue tip and a pure bitter sensation if placed in the region of the circumvallate papillæ; again, if leaves of a certain plant (*Gymnema sylvestre*) be chewed, the capacity to taste sweet or bitter things is lost for some time, but salts and acids are tasted as well as usual; and most persons taste salines better at the sides of the tongue than elsewhere.

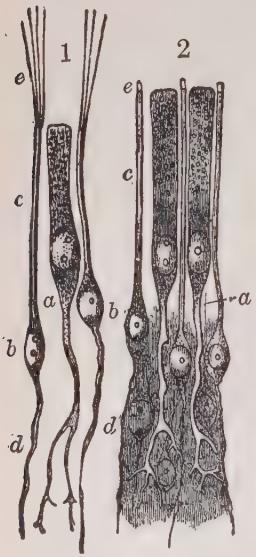


FIG. 76.—Cells from the olfactory epithelieum. 1, from the frog; 2, from man; *a*, columnar cell, with its branched deep process; *b*, olfactory cell; *c*, its narrow outer process projecting beyond the surface at *c*; *d*, its slender central process.

Smell. The olfactory organ proper consists of two small patches of epithelium (each about 250 mm. square) on the sides of a cleft formed by the nasal septum (the partition between the nostrils) on one side and the upper turbinate bone on the other. Intermingled with the columnar epithelial cells are true olfactory cells (*b*, Fig. 76); these are really modified sensory neurons; the peripheral portion (*c* and *e*, Fig. 76) corresponding to the dendron of an ordinary sensory neuron, and the central process, *d*, passing as an axon to a synaptic connection with an internuncial neuron in the *olfactory bulb* (I, Fig. 62). The clefts in which the olfactory patches are located are aside from the channels through which pass the main currents of air in breathing. The olfactory cells are therefore stimulated ordinarily only by such

odorous gases as diffuse to them from the main air currents. By the muscular act of "sniffing" the air current is sent more directly upon the olfactory patches, enhancing the keenness of smell.

Odorous substances, the stimuli of the olfactory apparatus, are always gaseous and frequently act powerfully when present in very small amount. We cannot, however, classify them by the sensations they arouse, or arrange them in series; and smells are but minor sensory factors in our mental life, although very powerful associations of memory are often aroused by odors. We commonly refer them to external objects, since we find that the sensation is intensified by "sniffing" air into the nose, and ceases when the nostrils are closed. Their peripheral localization is, however, imperfect, for we confound many smells with tastes (see below); nor can we well judge of the direction of an odorous body through the olfactory sensations which it arouses.

Although the sense of smell in man is aroused by inconceivably small amounts of odoriferous substance, one part of mercaptan to thirty billion of air being detectible, it is much less keen than the sense of smell in many animals, dogs in particular. In such animals the sense of smell as a source of information seems to be of the first importance, approaching our eyes in rank.

A striking thing about the sense of smell is the ease with which it is "fatigued." One may notice a bad odor upon entering a room, but in a few minutes ceases to perceive it because his olfactory apparatus has ceased to function. For this reason the sense of smell is wholly untrustworthy as a guide by which to regulate the ventilation of a room.

Many so-called tastes (flavors) are really smells; odoriferous particles of substances which are being eaten reach the olfactory region through the posterior nares and arouse sensations which, since they accompany the presence of objects in the mouth, we take for tastes. Such is the case, *e. g.*, with most spices; when the nasal chambers are blocked or inflamed by a cold in the head, or closed by compressing the nose, the so-called taste of spices is not perceived when they are eaten; all that is felt, when cinnamon, *e. g.*, is chewed under such circumstances is a certain pungency due to its stimulating nerves of touch in the tongue. This fact is sometimes taken advantage of in the practice of domestic medicine when a nauseous dose, as rhubarb, is to be given to a child.

CHAPTER XV

THE EYE AS AN OPTICAL INSTRUMENT

The Essential Structure of an Eye. Every visual organ consists primarily of a nervous expansion, provided with end organs by means of which light is enabled to excite nervous impulses, and exposed to the access of objective light; such an expansion in the higher animals is called a *retina*. By itself, however, a retina would give no visual sensations referable to distinctly limited external objects; it would enable its possessor to tell light from darkness, more light from less light, and (at least in its highly developed forms) light of one color from light of another color;

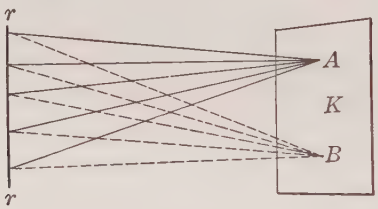


FIG. 77.—Diagram illustrating the indistinctness of vision with a retina alone. *K*, a surface on which are two spots, *A* and *B*; *r r*, the retina. The diverging lines represent rays of light spread uniformly over the retina from each spot.

but that would be all. Were our eyes merely retinas we could only tell a printed page from a blank one by the fact that, being partly covered with black letters (which reflect less light), it would excite our visual organ less powerfully than the spotless white page would. In order that distinct objects and not merely degrees of luminosity may be seen, some arrangement is needed which shall bring all light entering the eye from one point of a luminous surface to a *focus* again on one point of the sensitive surface. If *A* and *B* (Fig. 77) be two red spots on a black surface, *K*, and *rr* be a retina, then rays of light diverging from *A* would fall equally on all parts of the retina and excite it all a little; so with rays starting from *B*. The sensation aroused, supposing the retina in connection with the rest of the nervous visual apparatus, would be one

of a certain amount of red light reaching the eye; the red spots, as definite objects, would be indistinguishable. If, however, a convex glass lens L (Fig. 78) be put in front of the retina, it will cause to converge again to a single point all the rays from A falling upon it; so, too, with the rays from B: and if the focal distance of the lens be properly adjusted these points of convergence will both lie on the retina, that for rays from A at a, and that for rays from B at b. The sensitive surface would then only be excited at two limited and separated points by the red light emanating from

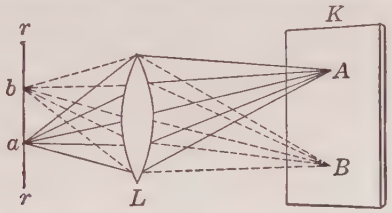


FIG. 78.—Illustrating the use of a lens in giving definite retinal images. A, B, K, r r, as in Fig. 78. L, a biconvex lens so placed that it brings to a focus on the points a and b of the retina, rays of light diverging from A and B respectively.

the spots; consequently only some of its end organs and nerve-fibers would be stimulated and the result would be the recognition of two separate red objects. In our eyes there are certain *refracting media* which lie in front of the retina and take the place of the lens L in Fig. 78. That portion of physiology which treats of the physical action of these media or, in other words, of the eye as an optical instrument, is known as the *dioptrics* of the eye.

The Appendages of the Eye. The eyeball itself consists of the retina and refracting media, together with supporting and nutritive structures and other accessory apparatuses, as, for example, some controlling the light-converging power of the media, and others regulating the size of the aperture (*pupil*) by which light enters. Outside the ball lie muscles which bring about its movements, and other parts serving to protect it.

Each orbit is a pyramidal cavity occupied by connective tissue, muscles, blood vessels, and nerves, and in great part by fat, which forms a soft cushion on which the back of the eyeball lies and rolls during its movements. The contents of the orbit being for the most part incompressible, the eye cannot be drawn into its

socket. It simply rotates there, as the head of the femur does in the acetabulum. When the orbital blood vessels are gorged, however, the eyeball may protrude (as in strangulation); and when these vessels empty it recedes somewhat, as is commonly seen after death. The front of the eye is exposed for the purpose of allowing light to reach it, but can be covered up by the *eyelids*, which are folds of integument, movable by muscles and strengthened by plates of fibrocartilage. At the edge of each eyelid the skin which covers its outside is turned in, and becomes continuous with a mucous membrane, the *conjunctiva*, which lines the inside of each lid, and also covers all the front of the eyeball as a closely adherent transparent layer.

The upper eyelid is larger and more mobile than the lower, and when the eye is closed covers all its transparent part. It has a special muscle to raise it, the *levator palpebræ superioris*. The eyes are closed by a flat circular muscle, the *orbicularis oculi* which, lying on and around the lids, immediately beneath the skin, surrounds the aperture between them. At their outer and inner angles (*canthi*) the eyelids are united, and the apparent size of the eye depends upon the interval between the canthi, the eyeball itself being nearly of the same size in all persons. Near the inner canthus the line of the edge of each eyelid changes its direction and becomes more horizontal. At this point is found a small eminence, the *lachrymal papilla*, on each lid. For most of their extent the inner surfaces of the eyelids are in contact with the outside of the eyeball, but near their inner ends a red vertical fold of conjunctiva, the *semilunar fold* (*plica semilunaris*) intervenes. This is a representative of the third eyelid, or *nictitating membrane*, found largely developed in many organisms, as birds, in which it can be drawn all over the exposed part of the eyeball. At the inner or nasal corner is a reddish elevation, the *caruncula lachrymalis*, caused by a collection of sebaceous glands * imbedded in the semilunar fold. Opening along the edge of each eyelid are from twenty to thirty minute compound sebaceous glands, named the Meibomian follicles. Their secretion is sometimes abnormally abundant, and then appears as a yellowish matter along the edges of the eyelids, which dries in the night and may cause the lids to be glued together in the morning. The *eyelashes* are short curved

* For a description of the glands see p. 569.

hairs, arranged in one or two rows along each lid where the skin joins the conjunctiva.

The Lachrymal Apparatus consists of the tear-gland in each orbit, the ducts which carry its secretion to the upper eyelid, and the canals by which the tears, except when excessive, are carried off from the front of the eye without running down over the face. The *lachrymal* or *tear-gland*, about the size of an almond, lies in the upper and outer part of the orbit, near the front end. It is a compound racemose gland (see Chap. XXIX), from which twelve or fourteen ducts run and open in a row at the outer corner of the upper eyelid. The secretion there poured out is spread evenly over the exposed part of the eye by the movements of winking, and keeps it moist; finally the tear is drained off by two *lachrymal canals*, one of which opens by a small pore (*punctum lachrymalis*) on each lachrymal papilla. The aperture of the lower canal can be readily seen by examining the corresponding papilla by the aid of a looking-glass. The canals run inwards and open into the *lachrymal sac*, which lies just outside the nose, in a hollow where the lachrymal and superior maxillary bones (*L* and *Mx*, Fig. 23) meet. From the sac the *nasal duct* proceeds to open into the nose-chamber, below the inferior turbinate bone and within the nostril.

Tears are constantly being secreted, but ordinarily only in such quantity as to be drained off into the nose, from which they flow into the pharynx and are swallowed. When the lachrymal ducts are stopped up, however, their continual presence makes itself unpleasantly felt, and many need the aid of a surgeon to clear the passage. In *weeping* the secretion is increased, and then not only more of it enters the nose, but some flows down the cheeks. The frequent swallowing movements of a crying child, sometimes spoken of as "gulping down his passion," are due to the need of swallowing the extra tears which reach the pharynx.

The Muscles of the Eye (Fig. 79). The eyeball is spheroidal, in form and attached behind to the optic nerve, *n*, somewhat as a cherry might be to a thick stalk. On its exterior are inserted the tendons of six muscles, four *straight* and two *oblique*. The straight muscles lie, one (*superior rectus*), *s*, above, one (*inferior rectus*), not appearing in the figure, below, one (*external rectus*), *a*, on the outer side, and one (*internal rectus*), *i*, on the inner side of

the eyeball. Each arises behind from the bony margin of the foramen through which the optic nerve enters the orbit. In the figure, which represents the orbits opened from above, the superior rectus of the right side has been removed. The *superior oblique* or *pulley* (*trochlear*) *muscle*, *t*, arises behind near the straight muscles and forms anteriorly a tendon, *u*, which passes through a fibro-cartilaginous ring, or pulley, placed at the notch in the frontal bone where it bounds superiorly the front end of the orbit. The tendon then turns back and is inserted into the eyeball between the upper and outer recti muscles. The *inferior oblique muscle* does not arise,

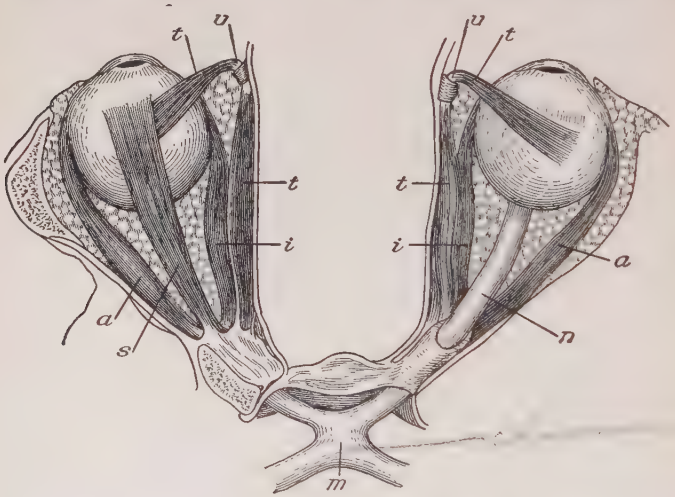


FIG. 79.—The eyeballs and their muscles as seen when the roof of the orbit has been removed and the fat in the cavity has been partly cleared away. On the right side the superior rectus muscle has been cut away. *a*, external rectus; *s*, superior rectus; *i*, internal rectus; *t*, superior oblique.

like the rest, at the back of the orbit, but near its front at the inner side, close to the lachrymal sac. It passes thence outwards and backwards beneath the eyeball to be inserted into its outer and posterior part.

The inner, upper, and lower straight muscles, the inferior oblique, and the elevator of the upper lid are supplied by branches of the third cranial nerve. The sixth cranial nerve goes to the outer rectus; and the fourth to the superior oblique.

The eye may be moved from side to side; up or down; obliquely,

that is, neither truly vertically nor horizontally, but partly both; or, finally, it may be rotated on its anteroposterior axis. The oblique movements are always accompanied by a slight amount of rotation. When the glance is turned to the left, the left external rectus and the right internal contract, and *vice versa;* when up, both superior recti; when down, both the inferior. The superior oblique muscle acting alone will roll the front of the eye downwards and outwards with a certain amount of rotation; the infe-

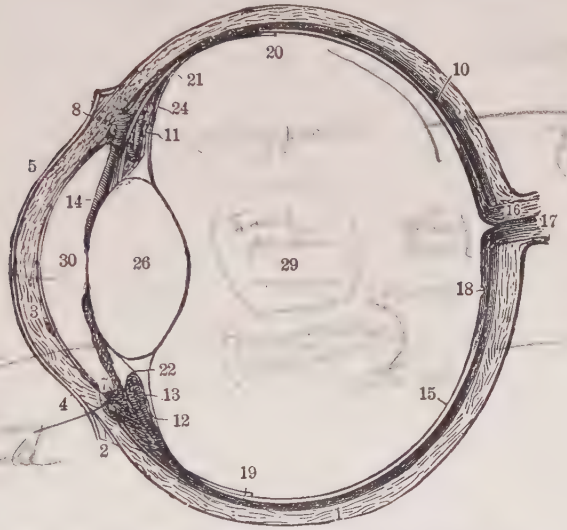


FIG. 80.—The left eyeball in horizontal section from before back. 1, sclerotic; 2, junction of sclerotic and cornea; 3, cornea; 4, 5, conjunctiva; 7, ciliary muscle; 10, choroid; 11, 13, ciliary processes; 14, iris; 15, retina; 16, optic nerve; 17, artery entering retina in optic nerve; 18, fovea centralis; 19, 20, region where sensory part of retina ends; 22, suspensory ligament; 24, the anterior part of the hyaloid membrane; 26, the lens; 29, vitreous humor; 30, aqueous humor.

rior oblique does the reverse. In oblique movements two of the recti are concerned, an upper or lower with an inner or outer; at the same time one of the oblique also always contracts. Movements of rotation rarely, if ever, occur alone.

The natural combined movements of the eyes by which both are directed simultaneously towards the same point depend on accurate adjustment of all their neuro-muscular apparatus. When the mechanism is so deficient that this adjustment cannot be made, and the eyes cannot be directed to a common point, the

person is said to *squint*. The squint may be due to paralysis of some muscle through disease of its motor nerve (p. 262) or of the brain center from which the nerve takes origin, or it may be due to inequalities in the lengths of the eye muscles. When all the eye muscles are of normal length the eyes at complete rest are slightly divergent, so that a small muscular effort (tonus) is always necessary to bring the axes of vision parallel, and a still larger effort to direct both eyes to a single near object. In many persons who do not actually suffer from squint one or another eye muscle may be longer or shorter than it should be; if the result is to make the axes more divergent than normal (*exophoria*) the greater effort needed to direct both eyes at one object is a fruitful source of eye-strain; similarly, when the axes are too convergent (*esophoria*) an effort is necessary whenever distant objects are looked at, and again eye-strain is likely to occur.

Dropping of the upper eyelid (*ptosis*) indicates paralysis of its special elevator muscle and is often a serious symptom, pointing to disease of the brain-parts from which it is innervated.

The Globe of the Eye is on the whole spherical, but consists of segments of two spheres (see Fig. 80), a portion of a sphere of smaller radius forming its anterior transparent part and being set on to the front of its posterior segment, which is part of a larger sphere. From before back it measures about 24 millimeters (1 inch), and from side to side about the same. Except when looking at near objects, the anteroposterior axes of the eyeballs are nearly parallel, though the optic nerves diverge considerably (Fig. 79); each nerve joins its eyeball, not at the center, but about 2.5 mm. (1/10 inch) on the nasal side of the posterior end of its anteroposterior axis. In general terms the eyeball may be described as consisting of three *coats* and three *refracting media*.

The outer coat, 1 and 3, Fig. 80, consists of the *sclerotic* and the *cornea*, the latter being transparent and situated in front; the former is opaque and white and covers the back and sides of the globe and part of the front, where it is seen between the eyelids as the *white* of the eye. Both are tough and strong, being composed of dense connective tissue.

The second coat consists of the *choroid*, 10, the *ciliary processes*, 11, 13, and the *iris*, 14. The *choroid* is made up of blood vessels supported by loose connective tissue containing numerous

corpuscles, which in its inner layers are richly filled with dark-brown or black pigment granules. Towards the front of the eyeball, where it begins to diminish in diameter, the choroid is thrown into plaits, the *ciliary processes*, 11, 13. Beyond these it continues as the *iris*, which forms the colored part of the eye seen through the cornea; and in the center of the iris is a circular aperture, the *pupil:* so its second coat does not, like the outer one, completely envelop the eyeball. In the iris is a ring of plain muscular tissue (sphincter) encircling the aperture of the pupil: when its fibers contract they narrow the pupil. Radiating from this ring to the edges of the iris are muscle-fibers which by their contraction enlarge the pupil. Both sets of muscles are under the control of autonomic nerves. Those to the sphincter reach the eye by way of the third cranial nerve and belong to the cranial autonomic system; those innervating the dilator enter by way of the ophthalmic branch of the fifth nerve. These latter fibers belong to the thoraco-lumbar autonomic system and have a rather tortuous connection with the central nervous system. The pathway starts in the upper thoracic region of the spinal cord where the cell-body of the preganglionic neuron lies. The axon of this neuron passes out from the cord to the sympathetic chain and in this chain up the neck to the superior cervical ganglion at the base of the skull. Here the preganglionic neuron terminates in connection with a post-ganglionic. The axon of the latter passes to the fifth nerve and along this to its termination in the dilator muscle.

The iris contains pigment which is yellow, or of lighter or darker brown, according to the color of the eye, and more or less abundant according as the eye is black, brown, or gray. In blue eyes the pigment is confined to the deeper layers, and modified in tint by light absorption in the anterior colorless strata through which the light passes.

The third coat of the eye, *the retina*, 15, is its essential portion, being the part in which the light produces those changes that give rise to impulses in the optic nerve. It is a still less complete envelope than the choroid, extending forwards only as far as the commencement of the ciliary processes, at least in its typical form. It is extremely soft and delicate; and, when fresh, transparent. Usually when an eye is opened the retina is colorless; but when an eye that has been in darkness is cut open in faint

yellow light and the exposed retina quickly examined in white light it is seen to be purple. The coloring substance (*visual purple*) very rapidly bleaches when a dead eye is exposed to daylight. On the front or inner surface of the human retina two special areas can be distinguished in a fresh eye. One is the point of entry of the optic nerve, 16, the fibers of which, penetrating the sclerotic and choroid, spread out in the retina. At this place the retina is whiter than elsewhere and presents an elevation, the *optic disk*. The other peculiar region is the *fovea centralis*, 18, which lies nearly at the posterior end of the axis of the eyeball and therefore outside the optic disk; in it the retina is thinner than elsewhere and so a pit is formed. This appears black, the thinned retina there allowing the choroid to be seen through it more clearly than elsewhere. In Fig. 81 is represented the right retina as seen from the front, the elliptical darker patch about the center indicating the fovea and the white circle on one side, the optic disk. The vessels of the retina arise from an artery (17, Fig. 80) which runs in with the optic nerve and from which branches diverge as shown in Fig. 81.

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FIG. 81.—The right retina as it would be seen if the front part of the eyeball with the lens and vitreous humor were removed.

The Optic Nerves, Chiasma, and Tracts. The optic nerves converge to meet in the optic chiasma (*m*, Fig. 79), from which the optic tracts pass to the region of the midbrain. They terminate mainly in the anterior corpora quadrigemina (superior colliculi) (Chap. IX), and in the corpora geniculata. The behavior of the nerve-fibers in the chiasma is interesting in that part of them cross to the opposite side and part continue into the tract of the same side. The fibers which cross over in each optic nerve are those coming from the inner half of the retina, the right half of the left retina and the left half of the right retina. The effect of this arrangement is to include in the right optic tract, behind the chiasma, the nerve-fibers from the right halves of both retinas,

and in the left optic tract those from the left halves of both retinas. Cutting the right optic nerve, therefore, causes total blindness of the right eye, but cutting the right optic tract blindness of the right half of each retina (*hemianopia*).

The half crossing of the optic nerve-fibers in man is correlated with the fact that his eyes are so placed that most of the field of vision is common to both. In mammals whose eyes are so laterally placed that at any given moment the objects seen by the two eyes are quite different, the crossing at the chiasma is complete; this condition obtains also in birds with the exception of owls, whose eyes like those of man have their visual axes parallel; in owls the crossing is only partial. It should be noted that the fovea centralis, which is the center of distinct vision, has nerve connections from both eyes with both optic tracts. For this reason unilateral injury to the visual mechanism back of the chiasma interferes practically not at all with ordinary vision, and sufferers from hemianopia may be unaware of their infirmity until careful examination by a physician reveals it.

The Microscopic Structure of the Retina. This, the sensitive portion of the eye, has the form of a thin membrane lining the entire back part of the cavity of the eyeball as far forward as the ciliary processes. Although only 0.15 millimeter (0.006 inch) thick it presents a very complex structure, ten distinct layers appearing upon microscopic examination. The membrane as a whole includes supporting tissues as well as sensitive and nervous tissues proper; we are concerned only with the latter and shall confine our discussion to them. The retina develops in such a way that the actual sensitive structures instead of being on its front surface where light would strike them immediately upon reaching the retina, are on its posterior surface, next to the choroid coat, and interposing between themselves and the source of light the nerve structures which connect them with the optic nerve, and the supporting tissues and blood vessels of the retina. Fortunately all these structures are so transparent or so placed as not to interfere seriously with vision. In the fovea, where all clear sight is located, blood vessels are absent and the other structures are much reduced.

The sensitive elements of the eye are called, from their shape, rods and cones. The rods consist of basal enlarged portions from which slender rod-like processes project toward the choroid coat.

These processes contain a peculiar reddish substance (*visual purple*), which has the property of bleaching out when exposed to light (*R*, Fig. 82). The cones have somewhat thicker basal portions than the rods and much shorter processes containing no visual purple (*C*, Fig. 82). Rods and cones make up layer number two of the ten retinal layers. The first layer, which is between

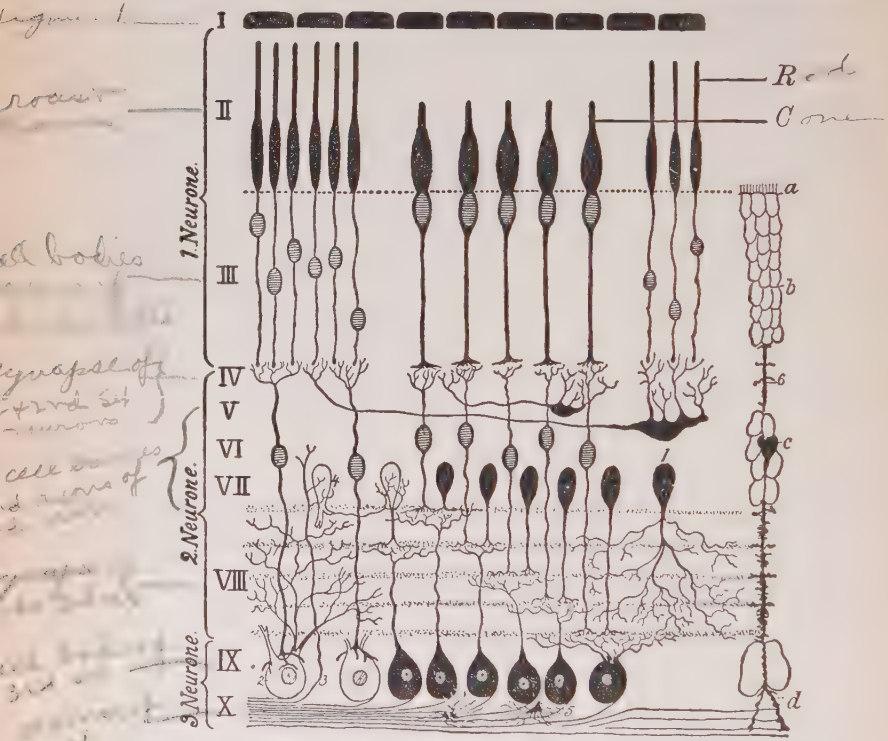


FIG. 82.—Diagram of the structure of the human retina (Greeff); *I*, pigment layer; *II*, rod and cone layer; *R*, rods; *C*, cones; *III-IX*, intraretinal nerve-elements; *X*, axons which pass to optic nerve.

the rods and cones and the choroid coat, is a layer of pigment cells which send processes in among the rods, and have something to do with forming the visual purple.

The rods and cones appear to constitute the peripheral or dendron portions of bipolar sensory neurons. They communicate with cell-bodies from which in turn pass typical, though very short, axons. The third retinal layer is composed of these

cell-bodies with their axons. The axons of the rod and cone neurons come into synaptic connection with dendrites of a second set of retinal neurons, the synapses making up the fourth retinal layer. The fifth, sixth, and seventh retinal layers contain the cell-bodies and short axons of these second retinal neurons; in the eighth layer these come into synaptic connection with the dendrites of the third set of retinal neurons. The large cell-bodies of these neurons make up the ninth retinal layer, and their axons, converging from all parts of the retina upon the optic disk, constitute the tenth and front layer of the retina. These axons continue uninterrupted to terminations in the midbrain ganglia. The relations of the three sets of retinal neurons are shown in the diagram (Fig. 82).

Rods and cones are not uniformly distributed over the retina. The fovea, where distinct vision is centered, contains only cones. The peripheral portions of the retina contain a larger and larger proportion of rods as the margin is approached, until the outermost regions contain only rods. This difference of distribution indicates a differentiation of function between the two sorts of sensitive structures. The probability of such differentiation is strengthened by the observation that each cone of the fovea communicates through the intervening retinal neuron with a single and separate neuron of the optic nerve, whereas the connection of the rods is such that several of them may send impulses into a single optic neuron.

The blood vessels of the retina lie almost entirely in the ninth and tenth retinal layers, *viz.*, along its front surface.

The Refracting Media of the Eye are, in succession from before back, the *aqueous humor*, the *crystalline lens*, and the *vitreous humor*.

The *aqueous humor* fills the space between the front of the lens, and the back of the cornea (30, Fig. 80). Chemically, it consists of water holding in solution a small amount of solid matters, mainly common salt.

The *crystalline lens* (26, Fig. 80) is colorless, transparent, and biconvex, with its anterior surface less curved than the posterior. It is surrounded by a capsule, and the inner edge of the iris lies in contact with it in front. In consistency it is soft, but its central layers are rather more dense than the outer.

The capsule is continuous at the margin of the lens with the *suspensory ligament* which in turn is attached all around to the ciliary processes. The suspensory ligament is stretched and its pull upon the capsule keeps the lens more flattened than it would be if free.

The *vitreous humor* (29, Fig. 80) is a soft jelly enveloped in a thin capsule, the *hyaloid membrane.* It consists mainly of water and contains some salts, a little protein, and some mucin. It is divided up, by delicate membranes, into compartments in which its more liquid portions are imprisoned.

The Ciliary Muscle. (7, Fig. 80.) Between the sclerotic and choroid coats, just where the former merges into the cornea, are small masses of smooth muscle-fibers which make up the ciliary muscle. These fibers are attached in front to the sclerotic coat and pass back a short distance to an insertion in the choroid coat just in front of the ciliary processes. The contraction of the ciliary muscle pulls the margin of the choroid coat forward and inward. The effect of this is to bring the ciliary processes nearer together and loosen the suspensory ligament, which is attached to them. The tension upon the capsule of the crystalline lens is thus diminished.

The ciliary muscle is interesting as being the only muscle in the Body innervated through the autonomic system over which we appear to have voluntary control.

The Properties of Light. Before proceeding to the study of the eye as an optical instrument, it is necessary to recall briefly certain properties of light.

Light is considered as a form of vibratory movement of a hypothetical medium, or "ether," the vibrations being in planes at right angles to the line of propagation of the light. Starting from a luminous point light travels in all directions along the radii of a sphere of which the point is the center; the light propagated along one such radius is called a *ray*, and in each ray the "ether" vibrates from side to side in a plane perpendicular to the direction of the ray.

Any ray, all of whose vibrations are at the same rate, is a ray of *monochromatic light.* It has a pure spectral color. The *wave length* of a beam of monochromatic light is measured by the distance between any phase of vibration and the first repetition

of precisely the same phase. Since the rate at which light travels in any given medium is constant, the wave length must vary inversely as the vibration rate. Light of high vibration rate has short wave length and vice versa. The color of monochromatic light depends upon its wave length. Where lights of various wave lengths are mixed together in a beam a *compound* light results. To the eye such a beam gives a definite color sensation but not one of the pure spectral colors.

Refraction. When light passes obliquely from one transparent medium into another of different density it is bent from its course, or refracted. The amount of refraction depends upon the optical nature of the two media and also upon the angle at which the ray strikes the surface of separation. This angle, measured between the incident ray and a line drawn at right angles to the surface between the media, is known as the angle of incidence. The angle which the refracted ray makes with this same perpendicular is the angle of refraction. If the ray is passing from a less refractive to a more refractive medium it is bent toward the perpendicular; if passing from a more to a less refractive medium it is bent away from the normal (Fig. 83). The amount of bending is determined by the *law* of *refraction* which is: *the ratio of the sine of the angle of incidence to that of the angle of refraction is always constant for the same two media and for light of the same wave length.*

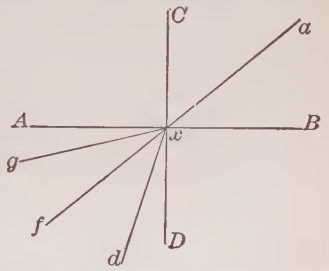


FIG. 83.—Diagram illustrating the refraction of light. *A B*, surface of separation between two transparent media; *C D*, the perpendicular to the surface at the point of incidence, *x*; *a x*, incident ray; *x d*, refracted ray, if the second medium be denser than the first; *x g*, refracted ray, if the second medium is less refractive than the first.

This ratio of sines is the *index* of *refraction*. It is usually expressed for various refractive media with air as the second and less refractive one.

Dispersion of Mixed Light. The shorter the vibration periods of light-rays the more they are deviated by refraction. Hence mixed light when sent through a prism is spread out, and decomposed into its simple constituents. For let *ax* (Fig. 84) be a ray of mixed light composed of a set of short and a set of long waves.

When it falls on the surface AB of the prism, that portion which enters will be refracted towards the perpendicular ED, but the short waves more than the longer. Hence the former will take the direction xy, and the latter the direction xz. On emerging from the prism both rays will again be refracted, but now from the normals Fy and Gz, since the light is passing from a more to a less refracting medium. Again the ray xy, made up of shorter waves, will be most deviated, as in the direction yv, and the long waves less, in the direction zr. If a screen were put at SS', we would receive on it at separate points, v and r, the two simple lights which

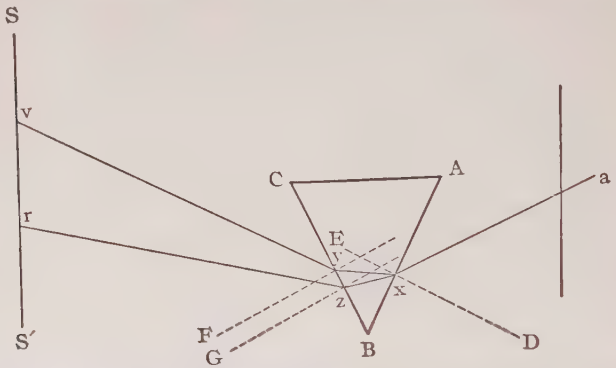


FIG. 84.—Diagram illustrating the dispersion of mixed light by a prism.

were mixed together in the compound incident ray ax. Such a separation of light-rays is called *dispersion*.

Ordinary white light, such as that of the sun, is composed of vibrations of every rate, mixed together. When such light is sent through a prism it gives a continuous band of light-rays, known as the *solar spectrum*, reaching from the least refracted to the most refracted and shortest waves. The exceptions to this statement due to Frauenhofer's lines (see Physics) are unessential for our present purpose. Not all the rays of the solar spectrum are visible to the human eye. The longest, called the infra red, and the shortest, the ultra violet, do not stimulate the retina; they are determined by their physical and chemical effects. The visible spectrum includes in order of increasing refrangibility the six spectral colors red, orange, yellow, green, blue, and violet (a seventh color, indigo, has often been assigned a place between blue and violet; presumably to satisfy a fancied necessity that the

rainbow have seven colors; as a matter of fact the eye makes no distinction between blue and indigo comparable to that between red and orange, for example). These colors merge insensibly into one another, showing the sun's light to be a mixture of all possible wave lengths, and not of certain selected ones.

Refraction of Light by Lenses. In the eye the refracting media have the form of lenses thicker in the center than towards the periphery; and we may here confine ourselves, therefore, to such *convex lenses*. If simple light from a point *A*, Fig. 78, fall on such a lens its rays, emerging on the other side, will take new directions after refraction and meet anew at a point, *a*, after which they again diverge. If a screen, *rr*, be held at *a* it will therefore receive an image of the luminous point *A*. For every convex lens there is such a point behind it at which the rays from a given point in front of it meet: the point of meeting is called the *conjugate focus* of the point from which the rays start. If instead of a luminous point a luminous object be placed in front of the lens an image of the object will be formed at a certain distance behind it, for all rays proceeding from one point of the object will meet in the conjugate focus of that point behind. The image is inverted, as can be readily seen from Fig. 85. All rays from the point *A* of the object meet at the point *a* of the image; those from *B* at *b*, and those from intermediate points at intermediate positions. If the single lens were replaced by several combined so as to form an *optical system* the general result would be the same, provided the system were thicker in the center than at the periphery.

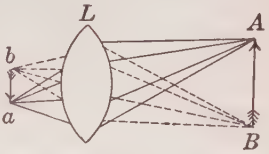


FIG. 85.— Diagram illustrating the formation of an image by a convex lens.

A moment's consideration of the diagram (Fig. 85) shows us that the nearer any luminous point is to the lens the further behind the lens its conjugate focus will be. The rays from near points are more divergent when they strike the lens than are those from far points, they are therefore not so much bent toward each other upon emerging, and their point of meeting is further back. There must be some point near the lens from which rays are so divergent that after emerging they do not meet at all, but continue to diverge or form a parallel beam. A plane so located with reference to a lens that rays from any point in it striking

the lens emerge in a parallel beam is the *principal focal plane* of the lens. The thicker a lens the nearer to it is its principal focal plane.

The Ordinary Photographic Camera is an instrument which serves to illustrate the formation of images by converging systems of lenses. It consists of a box blackened inside and having on its front face a tube containing the lenses; the posterior wall is made of ground glass. If the front of the instrument be directed on exterior objects, inverted and diminished images of them will be formed on the ground glass; those images only are well defined, at any one time, which are at such a distance in front of the instrument that the conjugate foci of points on them fall exactly on the glass behind the lens: objects nearer or farther off give confused and indistinct images; but by altering the distance between the lenses and the ground glass, in common language "focussing the instrument," either can be made distinct. For near objects the lenses must be farther from the surface on which the image is to be received, and for distant nearer.

The Refracting Media of the Eye Form a Convergent Optical System, made up of cornea, aqueous humor, lens, and vitreous

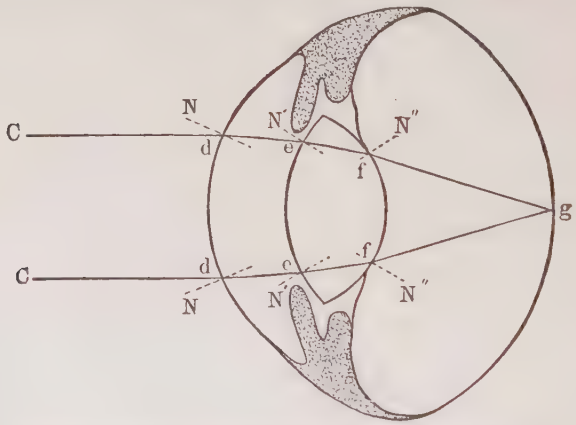


Fig. 86.—Diagram illustrating the surfaces at which light is refracted in the eye.

humor. These four media are reduced to three practically, by the fact that the indices of refraction of the cornea and aqueous humor are so nearly the same that they may be considered together as one converging lens. The surfaces at which refraction occurs are: (1) that between the air and the cornea; (2) that between the

aqueous humor and the front of the lens; (3) that between the vitreous humor and the back of the lens. The refractive indices of those media are: the air 1; the aqueous humor, 1.3379; the lens (average), 1.4545; the vitreous humor, 1.3379. From the laws of the refraction of light it therefore follows that (Fig. 86) the rays *Cd* will at the corneal surface be refracted towards the normals *N*, *N*, and take the course *de*. At the front of the lens they will again be refracted towards the normals to that surface and take the course *ef;* at the back of the lens, passing from a more refracting to a less refracting medium, they will be bent from the normals *N″* and take the course *fg*. If the retina be there, these parallel rays will therefore be brought to a focus on it. In the resting condition of the natural eye this is what happens to parallel rays entering it: and, since distant objects send into the eye rays which are practically parallel, such objects are seen distinctly without any effort, because all rays emanating from a point of the object meet again in one point on the retina.

Wide Range of Clear Vision in the Resting Eye. While in the normal resting eye only parallel rays focus exactly on the retina, the fact is that it sees clearly all objects that are as far as 18–20 feet away. The rays of light from points on such objects are divergent when they strike the cornea, and their focus is therefore behind the retina. How then can the resting eye see such objects clearly? The explanation is found in the structure of the retina. The light-perceiving elements, the rods and cones (Fig. 82), although extremely minute, are not mathematical points, but objects with measurable diameter. When light falls on one of them the effect is the same whether only a part of the element is illuminated or the whole, provided the light does not lap over into adjacent elements. Any beam of light entering the eye forms a cone with its apex at the focus. Near the focus a cross-section of the cone consists of a small circular area, which is larger the further away from the focus it is taken. Such an area is known as a *dispersion circle*. The convergent beams from the points of an object 18 feet away strike the retina before reaching their exact focus, but the dispersion circles formed by them are too small to stimulate more than one element; the effect is therefore the same as though an accurate focus had been reached, and objects at this distance are seen clearly.

Accommodation. Points on objects nearer than 18 feet send into the eye beams so diverging, and therefore focussing so far behind the retina, that the dispersion circles formed at the retina are too large to stimulate only single elements. Near objects, therefore, would not be seen distinctly, did not some change occur in the eye; since we can see them quite plainly if we choose (unless they be very near indeed), there must exist some means by which the eye is focussed or *accommodated* for looking at objects at different near distances. That some change does occur one can, also, readily prove by observing that we cannot see distinctly, at the same moment, both near and distant objects. For example, standing behind a lace curtain, at a window, we can as we choose look at

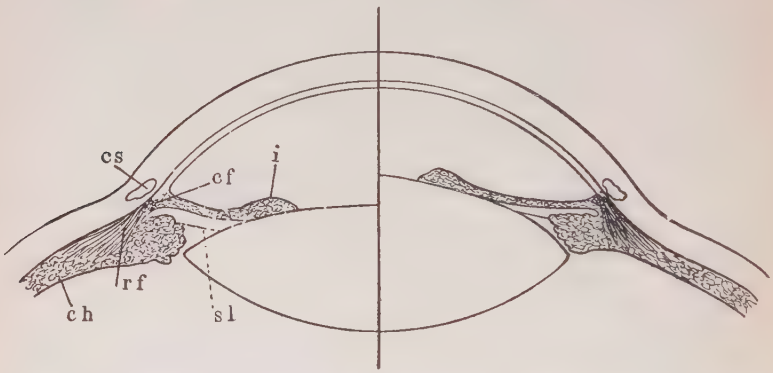


FIG. 87.—Diagram to illustrate the mechanism of accommodation; on the right half of the figure for a near, on the left for a distant, object; *rf*, ciliary muscle; *ch*, ciliary process of choroid; *sl*, suspensory ligament; *i*, iris.

the threads of the lace or at the houses across the street; but when we look at the one we see the other only indistinctly; and if, after looking at the more distant object, we look at the nearer we experience a distinct sense of effort. It is clear, then, that something in the eye is different in the two cases. The resting eye, suited for seeing distinctly distant objects, might conceivably be accommodated for near vision in several ways. The refracting indices of its media might be increased; that of course does not happen; the physical properties of the media are the same in both cases: or the distance of the retina from the refracting surfaces might be increased, for example, by compression of the eyeball by the muscles around it; however, experiment shows that changes of accommoda-

tion can, by stimulating the third cranial nerve, be brought about in the fresh excised eyes of animals from which the muscles lying outside the eyeball have been removed, in which no such compression is possible; we are thus reduced to the third explanation, that the refracting surfaces, or some of them, become more curved, and so bring diverging rays sooner to a focus. Observation shows that this is what actually happens: the corneal surface remains unchanged when a near object is looked at after a distant one, but the lens becomes considerably more convex.

Accommodation is brought about by the ciliary muscle (Fig. 87). In the resting eye it is relaxed and the suspensory ligament of the lens is taut, and, pulling on its edge, drags it out laterally a little and flattens its surfaces, especially the anterior, since the ligament is attached a little in front of the edge. To see a nearer object the ciliary muscle is contracted, and according to the degree of its contraction slackens the suspensory ligament, and then the elastic lens, relieved from the lateral drag, bulges out a little in the center.

When the eye is focussed for seeing a near object the circular muscle of the iris contracts, narrowing the pupil, but this has nothing directly to do with the accommodation.

Short Sight and Long Sight. In the normal eye parallel rays meet on the retina when the ciliary muscle is completely relaxed (*A*, Fig. 88). Such eyes are *emmetropic*. In other eyes the eye-ball is too long from before back; in the resting state parallel rays meet in front of the retina (*B*). Persons with such eyes, therefore, cannot see distant objects distinctly without the aid of diverging (concave) spectacles; they are *short-sighted* or *myopic*. Or the eyeball may be too short from before back; then, in the resting state, parallel rays are brought to a focus behind the retina (*C*). To see even infinitely distant objects, such persons must therefore use their accommodating apparatus to increase the converging power of the lens; and when objects are near they cannot, with the greatest effort, bring the divergent rays proceeding from them to a focus soon

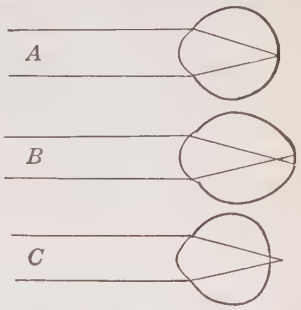


FIG. 88. — Diagram illustrating the path of parallel rays after entering an emmetropic (*A*), a myopic (*B*), and a hyperopic (*C*) eye.

enough. To get distinct retinal images of near objects they therefore need converging (convex) spectacles. Such eyes are called *hyperopic* or in common language *long-sighted.*

Optical Defects of the Eye. The eye, though it answers admirably as a physiological instrument, is by no means perfect optically; not nearly so good, for example, as a good microscope objective. The main defects in it are due to:

1. *Chromatic Aberration.* As already pointed out, the rays at the violet end of the solar spectrum are more refrangible than those at the red end. Hence they are brought to a focus sooner. The light emanating from a point on a white object does not, therefore, all meet in one point on the retina; but the violet rays come to a focus first, then the blue, and so on to the red, farthest back of all. If the eye is accommodated so as to bring to a focus on the retina parallel red rays, then violet rays from the same source will meet half a millimeter in front of it, and crossing and diverging there make a little violet *dispersion circle* around the red point on the retina. In optical instruments this defect is remedied by combining together lenses made of different kinds of glass; such compound lenses are called *achromatic.*

The general result of chromatic aberration, as may be seen in a bad opera-glass, is to cause colored borders to appear around the edges of the images of objects. In the eye we usually do not notice such borders unless we especially look for them; but if, while a transverse sash on a window with a white cloud in the background is looked at, a card be brought in front of the eye so as to cover half the pupil, colorations will be seen at the margin of sash with pane; yellowish if the sash is covered by the card and bluish if the pane. If accommodation be inexact they appear also when the boundary between a white and a black surface is observed. The phenomena due to chromatic aberration are much more easily seen if light containing only red and violet rays be used instead of white light containing all the rays of intermediate refrangibility. Ordinary blue glass only lets through these two kinds of rays. If a bit of it be placed over a very small hole in an opaque shutter and sunlight be admitted through the hole, it will be found that with one accommodation (that for the red rays) a red point is seen with a violet border, and with another (that at which violet rays are brought to a focus on the retina) a violet point is seen with a red aureole.

2. *Spherical Aberration.* It is not quite correct to state that ordinary lenses bring to a focus in one point behind them rays proceeding from a point in front, even when these are all of the same refrangibility. Convex lenses whose surfaces are segments of spheres, as are those of the eye, bring to a focus sooner the rays which pass through their marginal than those passing through their central parts. If rays proceeding from a point and traversing the lateral part of a lens be brought to a focus at any point, then those passing through the center of the lens will not meet until a little beyond that point. If the retina receive the image formed by the peripheral rays the others will form around this a small luminous circle of light—such as would be formed by sections of the cones of converging rays in Fig. 77, taken a little in front of *r r*. This defect exists in all glass lenses, as it is found impossible in practice to grind them of the nonspherical curvatures necessary to avoid it. In our eyes its effect is to a large extent corrected in the following ways: (*a*) The opaque iris cuts off many of the external and more strongly refracted rays, preventing them from reaching the retina. (*b*) The outer layers of the lens are less refracting than the central; hence the rays passing through its peripheral parts are less refracted than those passing nearer its axis.

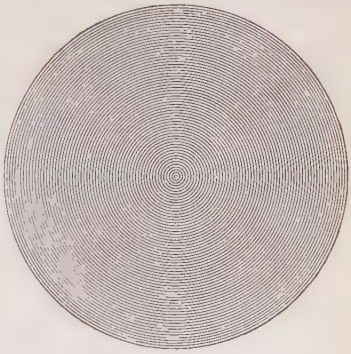


Fig. 89.

3. *Irregularities in Curvature.* The refracting surfaces of our eyes are not even truly spherical; this is especially the case with the cornea, which is very rarely curved to the same extent in its vertical and horizontal diameters. Suppose the vertical meridian to be the most curved; then the rays proceeding from points along a vertical line will be brought to a focus sooner than those from points on a horizontal line. If the eye is accommodated to see distinctly the vertical line, it will see indistinctly the horizontal and *vice versa*. Few people therefore see equally clearly at once two lines crossing one another at right angles. The phenomenon is most obvious, however, when a series of concentric circles (Fig. 89) is looked at: then when the lines appear sharp along some

sectors, they are dim along the rest. This defect is known as *astigmatism;* it is corrected by the use of lenses which are curved more in one plane than in the other. The lenses are so adjusted as to equalize the total refractive effect in the two planes.

4. *Opaque Bodies in the Refracting Media.* In diseased eyes the lens may be opaque (*cataract*) and need removal; or opacities from ulcers or wounds may exist on the cornea. But even in the best eye there are apt to be small opaque bodies in the vitreous humor causing *muscæ volitantes;* that is, the appearance of minute bodies floating in space outside the eye, but changing their position when the position of the eye changes, by which fact their origin in internal causes may be recognized. Many persons never see them until their attention is called to their sight by some weakness of it, and then they think they are new phenomena. Visual phenomena due to causes in the eye itself are called entoptic; the most interesting are those due to the retinal blood vessels (Chap. XVI). Tears, or bits of the secretion of the Meibomian glands, on the front of the eyeball often cause distant luminous objects to look like ill-defined luminous bands or patches of various shapes. The cause of such appearances is readily recognized, since they disappear or are changed after winking.

Hygienic Remarks. Since muscular effort is needed by the normal eye to see near objects, it is clear why the prolonged contemplation of such is more fatiguing than looking at more distant things. If the eye be hyperopic still more is this apt to be the case, for then the ciliary muscle has no rest when the eye is used, and to read a book at a distance such that the letters are large enough to be distinguished clearly requires an extraordinary effort of accommodation. Such persons complain that they can read well enough for a time, but soon fail to be able to see distinctly. This kind of weak sight should always lead to examination of the eyes by an oculist, to see if glasses are needed; otherwise severe neuralgic pains about the eyes are apt to come on, and the overstrained organ may be permanently injured. Astigmatism is another fruitful source of eye strain. Although sharp focussing is impossible the eye constantly strives for it. This involves great activity of the muscles of accommodation, which suffer from the effort. The occurrence of headache at frequent intervals, particularly in connection with the use of the eyes, as in reading or sew-

ing, is more often than not an indication of visual defects which proper glasses would overcome. Sufferers from such headaches should therefore have their eyes examined and if glasses are necessary should wear them.

Shortsighted persons are apt to have, or acquire, peculiarities of appearance: their eyes are often prominent, indicative of the abnormal length of the eyeball. They often stoop, too, from the necessity of getting their eyes near objects they want to see. The acquirement of such habits may be usually prevented by the use of proper glasses.

After middle life the lens begins to lose its elasticity, and no longer bulges freely in response to loosening of the suspensory ligament. The sign that this is beginning to happen is recession of the "near point," *i. e.*, the point closest to the face at which clear vision can be obtained by an extreme effort of accommodation. The effect is obviously to limit clear vision to such distances as the eye can be made to accommodate for; distant vision is not affected, only near vision. The condition is known as *presbyopia* or "old-sightedness." The correction is the same as for hyperopia, namely, a convex lens that will make up for the failure of the crystalline lens to shorten its focus sufficiently. Since distant vision is impossible through a lens that does this adequately, persons with presbyopia must either change to a special pair of "reading glasses" when looking at near objects, or wear "bi-focal" glasses, in which a small lens of proper curvature is set in the lower segment of ordinary glasses.

In all forms of defective vision improper glasses are as objectionable as none at all; skilled advice should therefore always be obtained when glasses are needed. The curvatures of the eyeball are subject to change; re-examination of the eyes at intervals is therefore usually necessary.

CHAPTER XVI

THE EYE AS A SENSORY APPARATUS

The Excitation of the Visual Apparatus. The excitable visual apparatus for each eye consists of the retina, the optic nerve, and the brain-centers connected with the latter; however stimulated, if intact, it causes visual sensations. In the great majority of cases its excitant is objective light, and so we refer all stimulations of it to that cause, unless we have special reason to know the contrary. As already pointed out pressure on the eyeball causes a luminous sensation, which suggests itself to us as dependent on a luminous body situated in space where such an object must be in order to excite the same part of the retina. Since all rays of light penetrating the eye, except in the line of its long axis, cross that axis, if we press the outer side of the eyeball we get a visual sensation referred to a luminous body on the nasal side; if we press below we see the luminous patch above, and so on.

Of course different rays entering the eye take different paths through it, but on general optical principles, which cannot here be

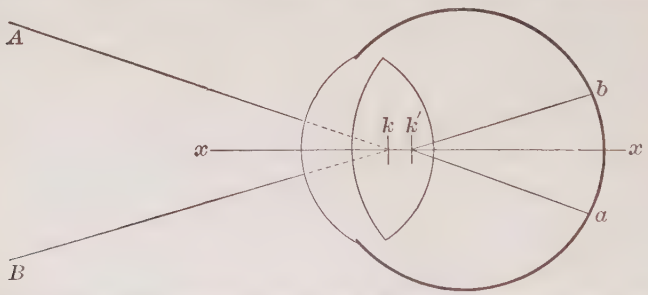


FIG. 90.—Diagram illustrating the points at which incident rays meet the retina. *xx*, optic axis; *k*, first nodal point; *k′*, second nodal point; *b*, point where the image of *B* would be formed, were the eye properly accommodated for it; *a*, the retinal point where the image of *A* would be formed.

detailed, we may trace all oblique rays through the organ by assuming that they meet and leave the optic axis at what are known as the *nodal points* of the system; these (*kk′*, Fig. 90) lie near together in the lens. If we want to find where rays of light from *A* will meet

the retina (the eye being properly accommodated for seeing an object at that distance) we draw a line from A to k (the first nodal point) and then another, parallel to the first, from k' (the second nodal point) to the retina. The nodal points of the eye lie so near together that for practical purposes we may treat them as one (k, Fig. 91), placed near the back of the lens. By manifold experience we have learnt that a luminous body (A, Fig. 91) which, we see, always lies on the prolongation of the line joining the ex-

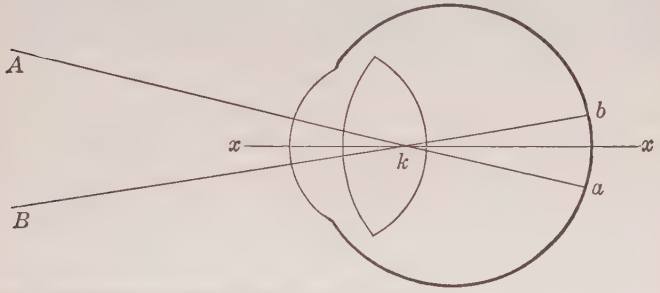


FIG. 91.—Diagrammatic section through the eyeball. xx, optic axis; k, nodal point.

cited part of the retina, a, and the nodal point k. Hence any excitation of that part of the retina makes us think of a luminous body somewhere on the line a A, and, similarly, any excitation of b, of a body on the line b B or its prolongation. It is only other conflicting experiences, as that with the eyes closed external bodies do not excite visual sensations, and the constant connection of the pressure felt on the eyelid with the visual sensation, that enable us when we press the eyeball to conclude that, in spite of what we seem to *see*, the luminous sensation is not due to objective light from outside the eye.

The Excitation of the Visual Apparatus by Light. Light only excites the retina when it reaches its nerve end organs, *the rods and cones*. The proofs of this are several.

1. *Light does not arouse visual sensations when it falls directly on the fibers of the optic nerve.* Where this nerve enters there is a retinal part possessing only nerve-fibers, and this part is blind. Close the left eye and look steadily with the right at the cross in Fig. 92, holding the book vertically in front of the face, and moving it to and fro. It will be found that at about 25 centimeters (10

inches) off the white circle disappears; but when the page is nearer or farther, it is seen. During the experiment the gaze must be kept fixed on the cross. There is thus in the field of vision a

Fig. 92.

blind spot, and it is easy to show by measurement that it lies where the optic nerve enters.

When the right eye is fixed on the cross, it is so directed that rays from this fall on the fovea (*y*, Fig. 93). The rays from the circle then cross the visual axis at the nodal point, *n*, and meet the retina at *o*. If the distance of the nodal point of the eye from the paper be *f*, and from the retina (which is 15 mm.) be *F*, then the distance, on the paper, of the cross from the circle will be to the distance of *y* from *o* as *f* is to *F*. Measurements made in this way show that the circle disappears when its image is thrown on the entry of the optic nerve, which lies to the nasal side of the fovea.

Fig. 93.

2. The above experiment having shown that light does not act directly on the optic nerve-fibers any more than it does on any other nerve-fibers, we have next to see in what part of the retina those changes do first occur which form the link between light and nervous impulses. *They occur in the outer part of the retina, in the rods and cones.* This is proved by what is called Purkinje's experiment. Take a candle into a dark room and look at a surface not covered with any special pattern, say a whitewashed wall or a plain window-shade. Hold the candle to the side of one eye and close to it, but so far back that no light enters the pupil from it; that is, so far back that the flame just cannot be seen, but so that a strong

light is thrown on the white of the eye as far back as possible. Then move the candle a little to and fro. The surface looked at will appear luminous with reddish-yellow light, and on it will be seen dark branching lines which are the shadows of the retinal vessels. Now in order that these shadows may be seen the parts on which the light acts must be behind the vessels, that is, in the layers of the retina next the choroid since the blood vessels lie in its front strata.

If the light be kept steady the vascular shadows soon disappear; in order to continue to see them the candle must be kept moving. The explanation of this fact may readily be made clear by fixing the eyes for ten or fifteen seconds on the dot of an "i" somewhere about the middle of this page: at first the distinction between the slightly luminous black letters and the highly luminous white page is very obvious; in other words, the different sensations arising from the strongly and the feebly excited areas of the retina. But if the glance be not allowed to wander, very soon the letters become indistinct and at last disappear altogether; the whole page looks uniformly grayish. The reason of this is that the powerful stimulation of the retina by the light reflected from the white part of the page soon fatigues the part of the visual apparatus it acts upon; and as this fatigue progresses the stimulus produces less and less effect. The parts of the retina, on the other hand, which receive light only from the black letters are but little stimulated and retain much of their original excitability, so that, at last, the feebler excitation acting upon these more irritable parts produces as much sensation as the stronger stimulus acting upon the fatigued parts; and the letters become indistinguishable. To see them continuously we must keep shifting the eyes so that the parts of the visual apparatus are alternately fatigued and rested, and the general irritability of the whole is kept about the same. So, in Purkinje's experiments if the position of the shadows remains the same, the shaded part of the retina soon becomes more irritable than the more excited unshaded parts, and its relative increase of irritability makes up for the less light falling on it, so that the shadows cease to be perceived. It is for this reason that we do not see the retinal vessels under ordinary circumstances. When light, as usual, enters the eye from the front through the pupil the shadows always fall on the same parts of the retina,

and these parts are thus kept sufficiently more excitable than the rest to make up for the less light reaching them through the vessels.

3. Further evidence that the rod and cone layer is the true receptor of the eye is furnished by the fact that the seat of most acute vision is the *fovea centralis*, where only this layer and the cone-fibers diverging from it are present. When we want to see anything distinctly we always turn our eyes so that its image shall fall on the foveæ.

The Intensity of Visual Sensations. Light considered as a form of energy may vary in quantity; physiologically, also, we distinguish quantitative differences in light as degrees of brightness, but the connection between the intensity of the sensation excited and the quantity of energy represented by the stimulating light is not a direct one. In the first place, some rays excite our visual apparatus more powerfully than others: a given amount of energy in the form of yellow light, for example, causes more powerful visual sensations than the same quantity of energy in the form of violet light.

Furthermore, the sense of vision, like all the other senses, obeys the psychophysical law (Chap. XIII). That is, differences of sensation are proportional not to absolute but to relative changes in the amount of stimulating energy. If a room is lighted by one candle and another is brought in we perceive an increase of illumination, but if it is lighted by an arc light the bringing in of a single lighted candle makes no perceptible difference in the illumination. The smallest difference in luminous intensity which we can perceive is about $\frac{1}{100}$ of the whole, for all the range of lights we use in carrying on our ordinary occupations. For strong lights the smallest perceptible fraction is considerably greater; finally we reach a limit where no increase in brightness is felt. For weak illumination the sensation is more nearly proportioned to the total differences of the objective light. Thus in a dark room an object reflecting all the little light that reaches it appears almost twice as bright as one reflecting only half; in a stronger light it would not so appear. Bright objects in general obscurity thus appear unnaturally bright when compared with things about them, and indeed often look self-luminous. A cat's eyes, for example, are said to "shine in the dark"; and painters to produce moonlight

effects always make the bright parts of a picture relatively brighter, when compared with things about them, than would be the case if a sunny scene were to be represented; by a relatively excessive use of white pigment they produce the relatively great brightness of those things which are seen at all in the general obscurity of a moonlight landscape.

Function of the Rods. Inasmuch as the rods are absent from the foveæ, they cannot be indispensable to clear vision, since this, as we know from experience, is confined to these areas. It is easy to demonstrate by a simple experiment that the parts of the retina containing rods are more susceptible to feeble lights than is the fovea, which is devoid of them. Just at twilight, when the first stars are seen faintly, one can readily pick out a star that disappears when looked at directly; if the gaze be turned to a point in the sky a degree or two to one side, so as to throw the image of the star off the fovea unto a rod-containing area, it becomes immediately visible again.

This evidence indicates that the function of the rods is somehow related to the reception of light stimuli of feeble intensity. The portions of the retina outside the fovea seem to function for the most part more reflexly than consciously; stimuli striking these portions of the retina bring about reflex movements of the eyes and head so that the source of stimulation throws its light upon the foveæ, and we derive conscious perceptions as to its nature. For such reflex activity a high degree of irritability is desirable.

It is said that some animals, such as snakes, have no rods in their retinas, while the retinas of others of nocturnal habits, such as owls, consist exclusively of rods.

Visual Purple. If a perfectly fresh retina be excised rapidly, its outer layers will be found of a rich purple color. In daylight this rapidly bleaches, but in the dark persists even when putrefaction has set in. In pure yellow light it also remains unbleached a long time, but in other lights disappears at different rates. If a rabbit's eye be fixed immovably and exposed so that an image of a window is focussed on the same part of its retina for some time, and then the eye be rapidly excised in the dark and placed in solution of potash alum, a colorless image of the window is found on the retina, surrounded by the visual purple of the rest

which is, through the alum, fixed or rendered incapable of change by light. Photographs, or *optograms*, are thus obtained which differ from the photographer's only in the nature of the chemical substances and processes involved. Both depend on the production of a chemical reaction by light. If the eye be not rapidly excised and put in the alum after its exposure, the optogram will disappear; the visual purple being rapidly regenerated at the bleached part. This reproduction of it is due to the cells of the pigmentary layer of the retina, which in living eyes exposed to light thrust long processes between the rods and cones. Portions of frogs' retinas raised from this, bleach more rapidly than those left in contact with it, but soon become purple again if let fall back upon the pigment-cells.

Dark- and Light-Adaptation. Common experience shows us that when we first go into a dimly lighted room we see less well than after being there a few minutes. To a slight extent the improvement is due to dilation of the pupils, by which more light enters the eye in the dark than in the light; but for the most part the effect is the result of an actual and very great increase in sensitiveness of the retinal rods, and a proportionally very much smaller increase in sensitiveness in the cones. The inability of the fovea to perceive faint lights is thus explained. The increase in sensitiveness in the rods is attributed to accumulation of visual purple in their external segments. The fact that only the rods become more sensitive harmonizes with the fact that in dim light extremely clear vision is less essential than perception of slight differences of illumination. In bright light the pupils contract sharply, excluding much light that would otherwise reach the retinas. The visual purple also bleaches out of the rods almost completely, and the pigment in the cells of the pigmentary layer retracts to their bases; the combined result is to decrease the sensitiveness of the rods to the minimum. The actual change in sensitiveness is amazingly large, being stated to amount to a ten-billion-fold increase from minimum to maximum. We need to recall, however, that the main function of the rods is to register changes in degree of illumination under whatever light conditions happen to prevail; furthermore that between dim light and extremely bright light the difference is also of the order of one to ten billion; thus through adaptation the mechanism

is able to function effectively over a wide range of levels of illumination.

The Duration of Luminous Sensations. This is greater than that of the stimulus, a fact taken advantage of in making fireworks: an ascending rocket produces the sensation of a trail of light extending far behind the position of the bright part of the rocket itself at the moment, because the sensation aroused by it in a lower part of its course still persists. So, shooting stars appear to have luminous tails behind them. By rotating rapidly before the eye a disk with alternate white and black sectors we get for each point of the retina on which a part of its image falls, alternating stimulation (due to the passage of a white sector) and rest (when a black sector is passing). If the rotation be rapid enough the sensation aroused is that of a uniform gray, such as would be produced if the white and black were mixed and spread evenly over the disk. In each revolution the eye gets as much light as if that were the case, and is unable to distinguish that this light is made up of separate portions reaching it at intervals: the stimulation due to each lasts until the next begins and so all are fused together. An excellent illustration of this is seen in the fact that in the "movies" the screen is actually illuminated only half the time.

The Localizing Power of the Retina. As already pointed out a necessary condition of seeing definite objects, as distinguished from the power of recognizing differences of light and darkness, is that all light entering the eye from one point of an object shall be focussed on one point of the retina. This, however, would not be of any use had we not the faculty of distinguishing the stimulation of one part of the retina from that of another part. This power the visual apparatus possesses in a very high degree; while with the skin we cannot distinguish from one, two points touching it less than 1 mm. ($\frac{1}{25}$ inch) apart, with our eyes we can distinguish two points whose retinal images are not more than .004 mm. (.00016 inch) apart. This depends on the enormous number and minute size of the retinal elements. Histological examination indicates a total number of rods ranging from 65,000,000 to 130,000,000, and of cones from 3,500,000 to 7,000,000. The distance between the retinal images of two points is determined by the "visual angle" under which they are seen; this angle is that

included between lines drawn from them to the nodal point of the eye. If a and b (Fig. 94) are luminous points, the image of a will be formed at a' on the prolongation of the line $a\ n$ joining a with the node, n. Similarly the image of b will be formed at b'. If a and b still remaining the same distance apart, be moved nearer the eye to c and d, then the visual angle under which they are seen will be greater and their retinal images will be farther apart, at c' and d'. If a and b are the highest and lowest parts of an object, the distance between their retinal images will then depend, clearly, not only on the size of the object, but on its distance from the eye;

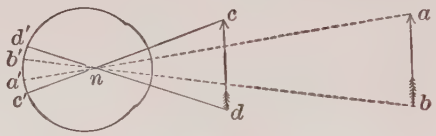


FIG. 94.

to know the discriminating power of the retina we must therefore measure the visual angle in each case. In the fovea centralis two objects seen under a visual angle of 50 to 70 seconds can be distinguished from one another; this gives for the distance between the retinal images that above mentioned, and corresponds pretty accurately to the diameter of a cone in that part of the retina. We may conclude, therefore, that when two images fall on the same cone or on two contiguous cones they are not discriminated; but that if one or more unstimulated cones intervene between the stimulated, the points may be perceived as distinct. The diameter of a rod or cone, in fact, marks the anatomical limit up to which we can by practice raise our acuteness of visual discrimination; and in the fovea which we constantly use all our lives in looking at things which we want to see distinctly, we have educated the visual apparatus up to about its highest power. Elsewhere on the retina our discriminating power is much less and diminishes as the distance from the fovea increases.

While we can tell the stimulation of an upper part of the retina from a lower, or a right region from a left, it must be borne in mind that we have no direct knowledge of which is upper or lower or right or left in the ocular image. All our visual sensations tell us is that they are aroused at different points, and nothing at all

about the actual positions of these on the retina. There is no other eye behind the retina looking at it to see the inversion of the image formed on it. Suppose I am looking out a pane in a second-story window at a distant house: its image will then fall on the fovea centralis; the line joining this with the pane is called the *visual axis*. The image of the roof will be formed on a part of the retina below the fovea, and that of the front door above it. I distinguish that the images of all these fall on different parts of the retina in certain relative positions, and have learnt, by the experience of all my life, that when the image of anything arouses the sensation due to excitation of part of the retina below the fovea the object is above my visual axis, and *vice versa;* similarly with right and left. Consequently I interpret the stimulation of lower retinal regions as meaning high objects, and of right retinal regions as meaning left objects, and never get confused by the inverted retinal image about which directly I know nothing. A newborn child, even supposing it could use its muscles perfectly, could not, except by mere chance, reach towards an object which it saw; it would grasp at random, not yet having learnt that to reach an object exciting a part of the retina above the fovea needed movement of the hand towards a position in space below the visual axis; but very soon it learns that things near its brow, that is *up*, excite certain visual sensations, and objects below its eyes others, and similarly with regard to right and left; in time it learns to interpret retinal stimuli so as to localize accurately the direction, with reference to its eyes, of outer objects, and never thenceforth is puzzled by retinal inversion.

Color Vision. Sunlight reflected from snow gives us a sensation which we call *white*. The same light sent through a prism and reflected from a white surface excites in us no *white* sensation but a number of color sensations, graduating insensibly from red to violet, through orange, yellow, green, and blue. The prism separates from one another light-rays of different wave-lengths and each ray excites in us a colored visual sensation, while all mixed together, as in sunlight, they arouse the entirely different sensation of white. If the light fall on a piece of black velvet we get still another sensation, that of black; in this case the light-rays are so absorbed that but few are reflected to the eye and the visual apparatus is left at rest. Physically black represents

nothing: it is a mere zero—the absence of ethereal vibrations; but, in consciousness, it is as definite a sensation as white, red, or any other color. We do not feel blackness or darkness except over the region of the possible visual field of our eyes. In a perfectly dark room we only feel the darkness in front of our eyes, and in the light there is no such sensation associated with the back of our heads or the palms of our hands, though through these we get no visual sensations. It is obvious, therefore, that the sensation of blackness is not due to the mere absence of luminous stimuli, but to the unexcited state of the retinas, which are alone capable of being excited by such stimuli when present. This fact is a very remarkable one, and is not precisely paralleled in any other sense. Physically, complete stillness is to the ear what darkness is to the eye; but silence impresses itself on us as the absence of sensation, while darkness causes a definite feeling of "blackness."

Our color sensations insensibly fade into one another; starting with black we can insensibly pass through lighter and lighter shades of gray to white: or beginning with green through darker and darker shades of it to black or through lighter and lighter to white: or beginning with red we can by imperceptible steps pass to orange, from that to yellow and so on to the end of the solar spectrum: and from the violet, through purple and carmine, we may get back again to red. Black and white appear to be fundamental color sensations mixed up with all the rest: we never imagine a color but as light or dark, that is, as more or less near white or black; and it is found that as the light thrown on any given colored surface weakens, the shade becomes deeper until it passes into black; and if the illumination be increased, the color becomes "lighter" until it passes into white. Of all the colors of the spectrum yellow most easily passes into white with strong illumination. Black and white, with the grays which are mixtures of the two, thus seem to stand apart from all the rest as the fundamental visual sensations, and the others alone are in common parlance named "colors."

Leaving aside black, white, gray, and the various browns (which are only dark tints of other colors), we may enumerate our color sensations as red, orange, yellow, green, blue, violet, and purple; between each there are, however, numerous transition shades, as yellow-green, blue-green, etc., so that the number

which shall have definite names given to them is to a large extent arbitrary. Of the above, all but purple are found in the spectrum given when sunlight is separated by a prism into its rays of different refrangibility; rays of a certain wave-length cause in us the feeling red; others yellow, and so on; for convenience we may speak of these as red, yellow, blue, etc., rays; all together, in about equal proportions, they arouse the sensation of white.

Peculiarities of Color Vision. A remarkable fact is that most color feelings can be aroused in several ways. White, for example, not only by the above general mixture, but red and blue-green rays, or orange and blue, or yellow and violet, taken in pairs in certain proportions, and acting simultaneously or in very rapid succession on the same part of the retina, cause the sensation of white: such colors are called *complementary* to one another. The mixture may be made in several ways; as, for example, by causing the red and blue-green parts of the spectrum to overlap, or by painting red and blue-green sectors on a disk and rotating it rapidly; they cannot be made, however, by mixing pigments, since what happens in such cases is a very complex phenomenon. Painters, for example, are accustomed to produce green by mixing blue and yellow paints, and some may be inclined to ridicule the statement that yellow and blue when mixed give white. When, however, we mix the pigments we do not combine the sensations of the same name, which is the matter in question. Blue paint is blue because it absorbs all the rays of the sunlight except the blue and some of the green; yellow is yellow because it absorbs all but the yellow and some of the green, and when blue and yellow are mixed the blue absorbs all the distinctive part of the yellow and the yellow does the same for the blue; and so only the green is left over to reflect light to the eye, and the mixture has that color. Grass-green has no complementary color in the solar spectrum; but with purple, which is made by mixing red and blue, it gives white. Several other colors taken three together, give also the sensation of white. If then we call the light-rays which arouse in us the sensation red, *a*, those giving us the sensation orange *b*, yellow *c*, and so on, we find that we get the sensation white with *a*, *b*, *c*, *d*, *e*, *f*, and *g*, all together; or with *b* and *e*, or with *c* and *f*, or with *a*, *d*, and *e;* our sensation *white* has no determinate relation to a given wave-length, and the same is true for several other colors;

yellow feeling, for example, may be excited by vibrations of one given wave-length (spectral yellow), or by a light containing only such waves as taken separately cause the sensations red and grass-green; in other words, a physical light in which there are no waves of the "yellow" length may cause in us the sensation yellow, which is only one more instance of the general fact that our sensations, as such, give us no direct information as to the nature of external forces; they are but signs which we have to interpret.

Function of the Cones. These structures, since they are the only sensitive elements of the fovea centralis, must be the receptors for all ordinary conscious vision. Their special function is doubtless the perception of color. This perception is a part of all our conscious visual sensations. We never think of a luminous object as being merely light; but always as having some color.

Distribution of Color Sense over the Retina. By means of an apparatus called the *perimeter* it is possible to determine the boundaries of visual sensation in the retina. In using this apparatus the subject with head supported in one position looks fixedly at a point straight in front; the observer then brings small squares of paper from the side toward the front and the subject reports the instant the square of paper comes into his field of vision. The angle is marked on a specially prepared chart and the observation repeated along different radii. By this means the field of vision is mapped out. The visual field for any particular color can be determined similarly, the subject in this case being required to report as soon as he is certain what the color of the square of paper is. Such studies have brought out the interesting fact that ability to perceive the different colors is unequally distributed over the retina. The margins of the visual field are sensitive only to white and black, and to their mixtures of gray; the fields for blue and yellow cover the whole area except the margins; the fields for red and green sensation are the smallest of all, occupying only the central part of the field and covering about half its entire surface. According to most determinations the boundaries of the yellow and blue fields do not coincide exactly, nor those of green and red; but if strictly complementary colors are used they are found to coincide very nearly.

It is clear from these observations that the cones in the central part of the visual field are sensitive to all colors; that those farther

out are sensitive to all except red and green; and that the margins, where cones are absent, are insensitive to color as such, and distinguish only degrees of light and darkness.

Color Blindness. This is a deficiency in color vision whereby certain colors fail to produce the characteristic color sensations that they do in normal eyes. The commonest sort of color blindness is so-called *red-green* blindness. In it neither red nor green has the same value as in normal eyes. Both colors seem to give the sensation of yellow, yellowish-brown, or gray. Two types are recognized: in *red-blindness* the red end of the spectrum is shortened and the maximum luminosity is not, as in normal eyes, in the yellow, but in the region which to normal eyes appears green, but in red-blindness appears gray or blue; in *green-blindness* the red end of the spectrum is not shortened and the maximum luminosity occurs where it does in normal eyes, namely, in the yellow; reds and greens are confused as in the red-blind.

Red-green blindness is the commonest form of defective color vision. It is practically always congenital and occurs more frequently in males than in females. On the average about four males in every hundred have the defect, while only about ten or twelve females in a thousand show it. This difference in incidence between the sexes is due to the fact that color vision is in heredity a sex-linked character. Its significance in that connection is described later (p. 611).

A form of *violet* blindness has been described as occurring in rare pathological conditions. It can be brought on temporarily, it is said, by taking the drug santonin. This form of color blindness has not been thoroughly studied. *Monochromatic* blindness, in which the only sensation is of degrees of grayness, shading at one end into white, at the other into black, is also described. This is accompanied in most cases by blindness of the fovea, and is probably therefore the result of complete loss of cone function.

A full explanation of red-green blindness cannot be had, of course, until the mechanism of color vision is understood. From what was said about the distribution of color perception in the retina it is clear, however, that in all eyes there is an area of red-green blindness between the area of complete color perception and the area of white-black vision. If we suppose the cones in the central area to be undifferentiated from those of this im-

mediately surrounding zone we have a condition of red-green blindness involving the whole eye and corresponding to that of the color-blind person.

The detection of color blindness is often a matter of considerable importance, especially in sailors and railroad operators since the two colors most commonly confounded, red and green, are those commonly used in maritime and railroad signals. Persons attach such different names to colors that a decision as to color blindness cannot be safely arrived at by simply showing a color and asking its name. A better plan is to take a heap of worsted of all tints, select one, say a red, and tell the man to put alongside it all those of the same color, whether of a lighter or a darker shade; if red blind he will select not only the reds but the greens, especially the paler tints, as well as the grays and browns. This test, which is widely used, was devised by the Swedish physiologist, Holmgren. Various other ingenious tests have also been devised and are in use in testing applicants for positions in train service and the like.

After-Images and Contrasts. These are well-marked visual phenomena, and have to be taken into account in attempting to explain the mechanism of color vision. After-images are visual sensations which remain after the withdrawal of the stimulus. They are best seen after looking at bright objects, or fixedly for several seconds at the same object. After-images are of two sorts, positive and negative. Positive after-images are always the same color as the object looked at; if one looks for an instant at an incandescent filament and then shuts his eyes he perceives a positive after-image of the filament. This is due, probably, to the persistence of the chemical process in the retina after the light which causes it is withdrawn. Negative after-images, instead of being the color of the object looked at, are always of its complementary color; if a red paper is looked at fixedly for several seconds and the eyes then turned to a white wall, a bluish green after-image is seen, instead of a red one. Negative after-images can also be seen by closing the eyes after looking fixedly at a bright object for some seconds.

Contrasts are effects produced by bringing side by side different colors; blue appears bluer when near yellow than when near other shades or the same shade of blue, and gray may appear blue when brought near yellow, both being dimmed slightly by overlying

tissue paper. Red and green heighten each other in a similar way. If a large black square and a large white square are placed side by side the black square looks blacker on the edge next the white than elsewhere, and the white looks whiter next the black than elsewhere.

Theories of Color Vision. A theory of color vision to be acceptable must explain first the fundamental facts of color perception, our ability to distinguish innumerable shades of color, and the fact that pairs or groups of fused colors give rise to sensations entirely unrelated to any of the constituent colors. The theory must account for the distribution of color perception over the retina and for the facts of color blindness; it must also explain after-images and contrasts. The fact that black, the absence of stimulation, has all the subjective qualities of a true sensation is also to be explained in some way. No theory yet proposed is satisfactory in accounting for all the known facts. Each one lays special emphasis on some group of visual phenomena and disregards such facts as cannot be harmonized with it. Three interesting theories will be briefly summarized for the sake of showing how such a problem is attacked. Each of them assumes that the excitation of the visual nerve endings depends upon the action of light upon certain *photochemical substances* in the cones.

The Young-Helmholtz Theory. This theory, proposed by Young in 1807 and elaborated by Helmholtz many years later, is the only one of the three that makes any attempt to reconcile the facts of color vision with the conception, fundamental in modern Physiology, that nerve impulses, however aroused, are much alike, and owe their particular effects in consciousness to the connections they make in the cerebral cortex.

The theory, as stated in terms of present-day nerve-physiology, assumes all our color sensations to be based on three primary ones, red, green, and violet, each of which is aroused by the decomposition of its special photochemical substance, and each having distinct nervous connection with the visual area of the cerebrum. Since anatomical study shows that each cone in the fovea has a single nerve-fiber leading from it we must suppose that there are three sorts of cones, one red-perceiving, one green-perceiving, and one violet-perceiving, and that these are scattered in groups of three over the retina.

According to this view any method of stimulating a red-perceiving cone would give rise to red sensations; if red- and green-perceiving cones were stimulated simultaneously the effect in consciousness would be very different from that of stimulating either one alone, the red cone and the green cone together, giving yellow; and if all three sorts were stimulated at once in equal amounts the effect would be a sensation of white. All our color perceptions are supposed to be based on proper combinations of stimuli acting on the groups of three cones. To explain some facts, such as that pure red light as it becomes brighter and brighter approaches and finally becomes white, the theory supposes that no light stimulates only one cone; all three of the group are stimulated by light of any color, and the effect in consciousness depends on which is more strongly stimulated.

When the theory was proposed it was thought that red-blindness and green-blindness were entirely distinct forms of color blindness. The theory fits that idea very well, since it supposes distinct red-perceiving and green-perceiving cones. Now that we know that both red and green blindness are really forms of red-green blindness in which neither red nor green gives normal color sensations the theory does not agree at all with the facts in this regard. The theory also fails to explain the distribution of color vision over the retina or the fact that black is a true sensation. It explains very well on the basis of fatigue the negative after-images that one sees when the eyes are turned to a white surface after looking at a colored body; for if one particular set of cones is fatigued by looking steadily at any color, white light coming upon the retina stimulates the unfatigued ones more powerfully than the fatigued ones, and instead of the sensation of white which follows equal stimulation of all cones, the complementary color to that which fatigued the cones in the first place is seen. The theory does not explain well the negative after-images seen with closed eyes, nor does it explain the phenomena of contrast.

The Hering Theory. This theory seeks to explain on a rational basis those visual phenomena which the Young-Helmholtz theory explains poorly or not at all. It is based upon the observation that whereas we recognize certain colors as being combinations of two others, as bluish-green, or reddish-yellow, there are no colors which we recognize as combinations of complementary colors; greenish-

red or yellowish-blue do not occur. The existence of these mutually exclusive colors suggested to the author of this theory that there might be two opposing processes going on in the retina, one a process of chemical breaking down or dissimilation; the other a process of building up, or assimilation.

He therefore postulated three photochemical substances, a white-black substance, a yellow-blue substance, and a red-green substance. He supposed that white light falling on the retina breaks down the white-black substance and gives rise to the sensation of white; whenever no white light is falling on the retina this substance is building itself up; this gives rise to the sensation of black. Similarly the sensation of red is the result of breaking down the red-green substance, and green of its assimilation. The white sensation resulting from stimulation of complementary colors is explained as due to neutralization of opposing effects. When red and green light come together into the retina the red-green substance is neither broken down nor built up. Both red and green light have a dissimilatory effect on the white-black substance as do rays of all colors, according to the theory. The only effect, therefore, of the complementary colors, is to produce a sensation of white. Contrast is explained as due to the maintenance of a sort of chemical balance in the retina whereby a breaking down of one of the elements in part of it is accompanied by building up of the same element in neighboring areas. So, if the yellow-blue substance is being broken down in part of the retina by yellow light, and built up in adjoining part by blue light, at the border between them each process is heightened by the near presence of the other.

The theory explains very well, also, the facts of negative after-images and of the distribution of color vision in the retina. The chief criticism that has been offered against it is that it apparently implies the necessity of one and the same nerve-fiber being able to convey a number of qualitatively different impulses. The same objection holds, although somewhat less forcibly, to the third of the theories to be described, which is primarily an attempt to combine the valuable features of the first two with certain new conceptions.

The Franklin Theory is based on the idea that the peculiar distribution of color vision over the retina is significant as suggesting

that the more complex color perceptions are evolved from simpler ones. According to this theory the primary photochemical substance is a gray-perceiving substance; white and black representing the ends of the gray color series. This substance is in all the rods, and in the cones of the retinal margin where only gray perception occurs. In the cones of the yellow-blue field, the fundamental gray-perceiving photochemical substance is supposed to be dissociated into two different photochemical substances, one yellow-perceiving, the other blue-perceiving. Since these are products of the gray-perceiving substance, when both are stimulated together the effect is the same as when the gray-perceiving substance itself is stimulated, namely, a shade of gray.

In the central cones of the retina a still further decomposition is assumed to have occurred, of the yellow-perceiving substance into red- and green-perceiving substances. The central cones, then, contain three photochemical substances, a red-perceiving one, a green-perceiving one, and a blue-perceiving one. Since all are ultimately derived from the gray-perceiving substance their combined stimulation produces gray sensations; simultaneous stimulation of the red and green substances gives the same result as stimulation of their parent substance. that for perceiving yellow.

This theory puts the distribution of color vision in the retina and the phenomenon of color blindness, which it explains as due to failure of dissociation of the yellow-perceiving substance, upon a more rational basis than do either of the other theories described. In most other respects it offers little advantage over them.

While we must admit that at present a full understanding of color vision is beyond us we may properly look forward to its ultimate mastery, as Physiology is able to penetrate more deeply the processes which underly it.

Visual Perceptions. The sensations which light excites in us we interpret as indications of the existence, form, and position of external objects. The conceptions which we arrive at in this way are known as *visual perceptions*. The full treatment of perceptions belongs to the domain of Psychology, but Physiology is concerned with the conditions under which they are produced.

The Visual Perception of Distance. With one eye our perception of distance is very imperfect, as illustrated by the common trick of

holding a ring suspended by a string in front of a person's face, and telling him to shut one eye and pass a rod from one side through the ring. If a penholder be held erect before one eye, while the other is closed, and an attempt be made to touch it with a finger moved across towards it, an error will nearly always be made. (If the finger be moved straight on towards the pen it will be touched because with one eye we can estimate direction accurately and have only to go on moving the finger in the proper direction till it meets the object.) In such cases we get the only clue from the amount of effort needed to "accommodate" the eye to see the object distinctly. When we use both eyes our perception of distance is much better; when we look at an object with two eyes the visual axes are converged on it, and the nearer the object the greater the convergence. We have a pretty accurate knowledge of the degree of muscular effort required to converge the eyes on all tolerably near points. When objects are farther off, their apparent size, and the modifications of their retinal images brought about by aërial perspective, come in to help. The relative distance of objects is easiest determined by moving the head; all stationary objects then appear displaced in the opposite direction (as for example when we look out of the window of a railway car) and those nearest most rapidly; from the different apparent rates of movement we can tell which are farther and nearer. We so inseparably and unconsciously bind up perceptions of distance with the sensations aroused by objects looked at, that we seem to see distance; it seems at first thought as definite a sensation as color. That it is not, is shown by cases of persons born blind, who have had sight restored later in life by surgical operations. Such persons have at first no visual perceptions of distance: all objects seem spread out on a flat surface in contact with the eyes, and they only learn gradually to interpret their sensations so as to form judgments about distances, as the rest of us did unconsciously in childhood before we thought about such things.

The Visual Perception of Size. The dimensions of the retinal image determine primarily the sensations on which conclusions as to size are based; and the larger the visual angle the larger the retinal image; since the visual angle depends on the distance of an object the correct perception of size depends largely upon a correct perception of distance; having formed a judgment, conscious or

unconscious, as to that, we conclude as to size from the extent of the retinal region affected. Most people have been surprised now and then to find that what appeared a large bird in the clouds was only a small insect close to the eye; the large apparent size being due to the previous incorrect judgment as to the distance of the object. The presence of an object of tolerably well-known height, as a man, also assists in forming conceptions (by comparison) as to size; photographers of natural wonders therefore frequently introduce human figures to assist in giving an idea of the size of other objects represented.

The Visual Perception of a Third Dimension of Space. This is very imperfect with one eye; still we can thus arrive at conclusions from the distribution of light and shade on an object, and so get that amount of knowledge as to the relative distance of different points which is attainable monocularly; the different visual angles under which objects are seen also assist us in concluding that objects are farther and nearer, and so are not spread out on a plane before the eye, but occupy depth also. Painters depend mainly on devices of these kinds for representing solid bodies, and objects spread over the visual field in the third dimension of space.

Single Vision with Two Eyes. When we look at a flat object with both eyes we get a similar retinal image in each. Under ordinary circumstances we see, however, not two objects but one. In the habitual use of the eyes we move them so that the images of the object looked at fall on the two foveæ. A point to the left of this object forms its image on the inner (right) side of the left eye and the outer (right) side of the right. An object vertically above that looked at would form an image straight below the fovea of each eye; an object to the left and above, its image to the inner side and below in the left eye and to the outer side and below in the right eye; and so on. We have learned that similar simultaneous excitations of these *corresponding points* mean single objects, and so interpret our sensations. When the eyes do not work together, as in the muscular inco-ordination of one stage of intoxication, then they are not turned so that images of the same objects fall on corresponding retinal points, and the person sees double. When a squint comes on, as from paralysis of the external rectus of one eye, the sufferer sees double for the same reason.

When a given object is looked at, lines drawn from it through the nodal points reach the fovea centralis in each eye. Lines so drawn at the same time from a more distant object diverge less and meet each retina on the inner side of its fovea; but as above pointed out the corresponding points for each retinal region on the inside of the left eye, are on the outside of the right, and *vice versa*. Hence the more distant object is seen double. So, also, is a nearer object, because the more diverging lines drawn from it through the nodal points lie outside of the fovea in each eye. Most people go through life unobservant of this fact; we only pay attention to what we are looking at, and nearly always this makes its images on the two foveæ. That the fact is as above stated may, however, be readily observed. Hold one finger a short way from the face and the other a little farther off; looking at one, observe the other without moving the eyes; it will be seen double. For every given position of the eyes there is a surface in space, all objects on which produce images on corresponding points of the two retinas: all objects in it are seen single; all others in the visual field, double.

The Perception of Solidity. When a solid object is looked at the two retinal images are different. If a truncated pyramid be held in front of one eye its image will be that represented at *P*, Fig. 95.

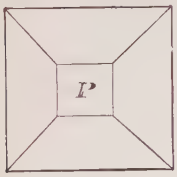
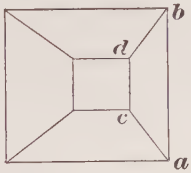


Fig. 95.



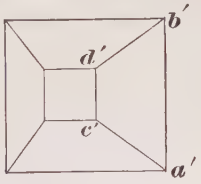


Fig. 96.

If, however, it be held midway between the eyes, and looked at with both, then the left-eye image will be that at the left of Fig. 96, and the right-eye image that at the right. The small surface, *b d c a*, in one answers to the large surface, *b′ d′ c′ a′*, in the other. This may be readily observed by holding a small cube in front of the nose and alternately looking at it with each eye. In such cases, then, the retinal images do not correspond, and yet we combine them in consciousness so as to see one *solid* object. This is known as *stereoscopic vision*, and the illusion of the common

stereoscope depends on it. Two photographs are taken of the same object from two different points of view, one as it appears when seen from the left, and the other when seen from the right. These are then mounted for the stereoscope so that each is looked at by its proper eye, and the object appears in distinct relief, as if, instead of flat pictures, solid objects, occupying three dimensions of space, were looked at.

CHAPTER XVII

THE STRUCTURE AND FUNCTIONS OF TISSUE FLUID, BLOOD, AND LYMPH

Introductory. We turn at this point from study of the mechanisms by which the Body adapts itself to its surroundings to a consideration of the structures and processes engaged in body maintenance. These have the task of providing the living tissues of the Body with supplies of energy-yielding material and of keeping them in good working order. Their dependence upon the environment is not so obvious perhaps as is that of the adaptive mechanisms proper, although as a matter of fact, changes in the environment do influence the maintenance mechanisms, and often very promptly and strikingly. For example, variations in the surrounding temperature bring about adaptive responses in the mechanism for keeping the Body at the proper degree of warmth. We shall have constant occasion, therefore, to recall the facts brought out in preceding chapters.

The External Medium. During the whole of life interchanges of material go on between every living being and the external world; by these exchanges material particles that at one time constitute parts of inanimate objects come at another to form part of a living being; and later on these same atoms, after having been a part of a living thing, are passed out from it in the form of lifeless compounds. As the foods and wastes of various organisms differ more or less, so are more or less different environments suited for their existence; and there is accordingly a relationship between the plants and animals living in any one place and the conditions of air, earth, and water prevailing there. Even such simple unicellular animals as the amœbæ live only in water or mud containing in solution certain gases, and in suspension solid food-particles; and they soon die if the water be changed either by essentially altering its gases or by taking out of it the solid food. So in yeast we find a unicellular plant which thrives and multiplies only in liquids of certain composition, and which

in the absence of organic compounds of carbon in solution will not grow at all. Each of these simple living things, which corresponds to one only of the innumerable cells composing the full-grown Human Body, thus requires for the manifestation of its vital properties the presence of a surrounding medium suited to itself: the yeast would die, or at the best lie dormant, in a liquid containing only the solid organic particles on which the amœba lives; and the amœba would die in such solutions as those in which yeast thrives best.

The Internal Medium. A similar close relationship between the living being and its environment, and an interchange between the two like that which we find in the amœba and the yeast-cell, we find also in even the most complex living beings. When, however, an animal comes to be composed of many cells, some of which are placed far away from the surface of its body and from immediate contact with the environment, there arises a new need—a necessity for an internal medium or *body fluid* which shall play the same part toward the individual cells as the surrounding air, water and food to the whole animal. A portion of this internal medium is kept in movement, and receives at some regions of the bodily surfaces materials from the exterior, while losing substances to the exterior at the same or other surfaces, thus forming a sort of middleman between the individual tissues and the surrounding world; the medium as a whole stands in the same relationship to each of the cells of the Body as the water in which an amœba lives does to that animal, or its nutrient medium does to a yeast-cell. We find accordingly the Human Body pervaded by a liquid, containing gases and food-material in solution, the presence of which is necessary for the maintenance of the life of the tissues. Any great change in this medium will affect injuriously few or many of the groups of cells in the Body, or may even cause their death; just as altering the media in which they live will kill an amœba or a yeast-cell.

In a body so large and complex as that of man, moreover, the internal medium must do more than merely bring food to the individual cells and carry waste materials away from them. All the cells have to be kept at just the right degree of warmth, but some produce more heat than others; so part of its work is to maintain an even distribution of heat over the whole Body or

when excess is generated to provide for its escape. Many metabolic processes, particularly the fundamental ones that make up basic metabolism, and the slow processes of growth, are not of a nature to be controlled by the nervous system. Their control is vested in the *hormones* with which we are already familiar. These are conveyed by the internal medium to all parts of the Body, being thus sure of reaching the structures upon which their influence is to be exerted. Finally, the environment which is favorable for the life and growth of the body-cells is also favorable for the life and growth of foreign and harmful organisms. That the Body is subject to invasion by such organisms is only too well known, and but for the system of defense which the internal medium affords these invasions could not fail to be even more disastrous than they are.

We can summarize the functions of the internal medium as follows:

1. To convey to all the living cells their needed supplies of food material and oxygen.
2. To convey away from the body-cells the waste materials generated by their activities.
3. To distribute heat uniformly over the Body and provide for getting rid of the excess.
4. To convey from the regions where they are produced to those where they are used the special substances, *hormones,* which regulate many bodily processes.
5. To defend the Body against the inroads of disease-producing micro-organisms.

The Blood. In the Human Body the internal medium is composed in part of fluid that bathes the cells immediately, and is known as *tissue fluid* (p. 30); this fluid is relatively stationary. Separated from the tissue fluid by being inclosed in the blood-vessels is the remainder of the internal medium, the *blood.* Although many of the tissues appear very compact there are none so dense as not to have interstices among the cells into which tissue fluid penetrates. Furthermore there are very few portions of the Body into which the blood is not carried. One of the exceptions is the epidermis or outer layer of the skin: if a cut be made through it only, leaving the deeper skin-layers intact, no blood will flow from the wound. Hairs and nails also contain no blood. In the in-

terior of the Body the epithelial layers lining free surfaces, such as the inside of the alimentary canal, contains no blood, nor do the hard parts of the teeth, the cartilages, and the refracting media of the eye (see Chap. XV), but these interior parts are moistened with liquid of some kind, and unlike the epidermis are protected from rapid evaporation. All these bloodless parts together form a group of *non-vascular tissues;* they alone excepted, a wound of any part of the Body will cause bleeding.

Relation Between Blood and Tissue Fluid. As already pointed out (p. 306) the individual cells derive their supplies from the tissue fluid in which they are bathed and pour out their wastes into the same. A fact that has not yet been stressed is that in the Human Body the total amount of living protoplasm is several times greater than the amount of tissue fluid; in other words, the cells are much bulkier than the spaces among them. It follows that as the cells carry on their metabolism they draw continuously on relatively very small depots for the needed materials, and at the same time pour out waste products into receiving areas of very small capacity. Obviously this could not go on very long unless some arrangement were present for renewing the tissue fluids as fast as depleted of supplies, and of removing the wastes as fast as they accumulate. The channel of renewal is the blood, which is inclosed in a set of tubes and by action of a pump, the *heart,* kept circulating in a definite course which brings it in turn first into relationship with the tissue fluids, and then with special maintenance regions (respiratory, digestive, hormone-providing, temperature-regulating, and excretory). This round is made over and over again; thus what the blood loses in one region it regains in another. The situation is represented diagrammatically in Fig. 97.

Phenomena of filtration and dialysis (p. 31) play a great part in the nutritive processes of the Body. The tissue fluid present in any organ gives up things to the cells there and gets things from them; and thus, although it may have originally been tolerably like the liquid part of the blood, it soon acquires a different chemical composition. Dialysis then commences between the tissue fluid outside and the blood inside the minute blood vessels known as capillaries, and the latter gives up to the tissue fluid new materials in place of those which it has lost and takes from it

the waste products it has received from the tissues. When this blood, altered by exchanges with the tissue fluid, gets again to the neighborhood of the digestive tract, having lost some food-materials it is poorer in these than the richly supplied tissue fluid around the cells of this tract, and takes up a supply by dialysis from them. When it reaches the excretory organs it has previously picked up a quantity of waste matters and loses these by dialysis to the tissue fluid there present, which is specially poor in such matters, since the excretory cells constantly deprive

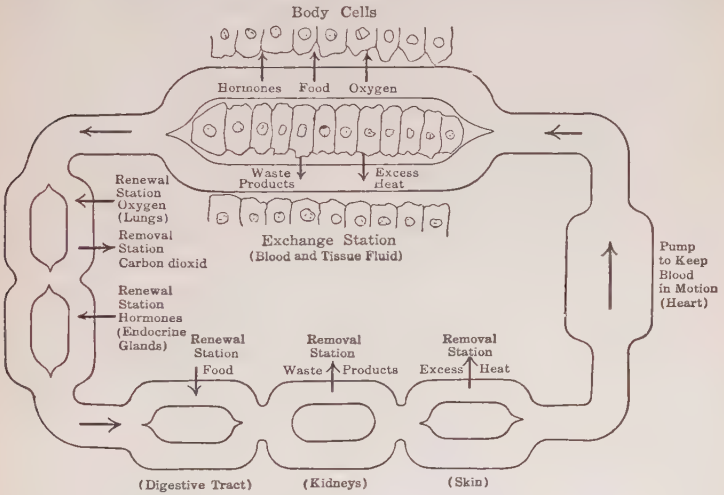


FIG. 97.—Diagram to illustrate how suitable cell-environment is maintained by the flow of blood through a series of capillaries, tissue fluid being renewed at the expense of the blood, and the blood being renewed in turn during its passage through the vessels of lungs, endocrine glands, digestive tract, kidneys, and skin.

it of them. In consequence of the different wants and wastes of various cells, and of the same cells at different times, the tissue fluid must vary considerably in composition in various organs of the Body, and the blood flowing through them will gain or lose different things in different places. But renewing during its circuit in one what it loses in another, its average composition is kept pretty constant, and, through interchange with it, the average composition of the tissue fluid also.

The Lymph. The blood, on the whole, loses more liquid to the tissue fluid through the capillary walls than it receives back the same way. This depends mainly on the fact that the pressure

on the blood inside the vessels is greater than that outside, and so a certain amount of filtration of liquid from within out occurs through the vascular wall in addition to the dialysis proper. The excess is collected from the various organs of the Body into a set of *lymphatic vessels* which carry it directly back into some of the larger blood vessels near where these empty into the heart; after entry into these lymphatic vessels the fluid is known as *lymph;* in this way the liquid which is forced out of the blood stream in the capillaries gets back into it again.

The Lacteals. In the walls of the alimentary canal certain food-materials after passing through the cells into the tissue fluid are not transferred locally, like the rest, by dialysis into the blood, but are carried off bodily in the lymph-vessels and poured into the veins of a distant part of the Body. The lymphatic vessels concerned in this work, being frequently filled with a white liquid during digestion, are called the *milky* or *lacteal vessels.*

Summary. To sum up: the tissue fluid and blood form the internal medium in which the tissues of the Body live; the tissue fluid is primarily derived from the blood and forms the immediate medium for the great majority of the living cells of the Body; and the excess of it is finally returned to the blood in the form of lymph. The tissue fluid is almost stationary, but is constantly renovated by the blood, which is kept in rapid movement, and which, besides containing a store of new food-matters, carries off the wastes which the various cells have poured out, and thus is also a sort of sewage stream into which the wastes of the whole Body are primarily collected.

Composition of the Blood. The average specific gravity of human blood is 1,055. It has a slightly alkaline reaction. Nearly half its mass consists of moist corpuscles and the remainder of the liquid part or plasma. Exposed in a vacuum, 100 volumes of blood yield about 60 of gas consisting of a mixture of oxygen, carbon dioxid, and nitrogen.

Microscopic Characters of Blood. If a finger be pricked, and the drop of blood flowing out be spread on a glass slide, covered, protected from evaporation, and examined with a microscope magnifying about 400 diameters, it will be seen to consist of innumerable minute bodies floating in a liquid. The bodies are the *blood-corpuscles,* and the liquid is the *blood-plasma.*

The corpuscles are not all alike. While currents still exist in the freshly-spread drop of blood, the great majority of them are readily carried to and fro; but a certain number more commonly stick to the glass and remain in one place. The former are the *red*, the latter the *pale* or *colorless blood-corpuscles*. With proper precautions a third sort of corpuscles, the blood-plates, may also be seen.

Red Corpuscles. *Form and Size.* The red corpuscles or *erythrocytes* as they float about frequently seem to vary in form, but

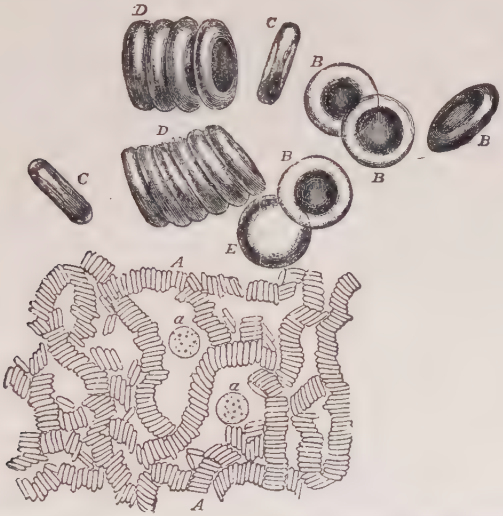


FIG. 98.—Red blood-corpuscles. *A*, magnified about 400 diameters. The red corpuscles have arranged themselves in rouleaux; *a*, *a*, colorless corpuscles; *B*, red corpuscles more magnified and seen in focus; *E*, a red corpuscle slightly out of focus. Near the right-hand top corner is a red corpuscle seen in three-quarter face, and at *C* one is seen edgewise.

by a little attention it can be made out that this appearance is due to their turning round as they float, and so presenting different aspects to view; just as a silver dollar presents a different outline according as it is looked at from the front or edgewise or in three-quarter profile.

Sometimes the corpuscle (Fig. 98, *B*) appears circular; then it is seen in full face; sometimes linear (*C*), and slightly narrowed in the middle; sometimes oval, as the dollar when halfway between a full and a side view. These appearances show that each red

corpuscle is a circular disk, slightly hollowed in the middle (or biconcave) and about four times as wide as it is thick. The average transverse diameter is 0.008 millimeter ($\frac{1}{3200}$ inch). Shortly after blood is drawn the corpuscles tend to arrange themselves in rows, or *rouleaux*, adhering to one another by their broader surfaces.

Color. Seen singly each red corpuscle is of a pale yellow color; it is only when collected in masses that they appear red. The blood owes its red color to the great numbers of these bodies in it; if it is spread out in a very thin layer it, too, is yellow.

Structure. So far as optical analysis goes each corpuscle is homogeneous throughout. By other means we can, however, show that at least two materials enter into the structure of each red corpuscle. If the blood be diluted with several times its own bulk of water and examined with the microscope, it will be found that the formerly red corpuscles are now colorless and the plasma colored. The dilution has caused the coloring matter to pass out of the corpuscles and dissolve in the liquid. This coloring constituent of the corpuscle is *hemoglobin*, and the colorless residue which it leaves behind and which swells up into a sphere in the diluted plasma is the *stroma*. In the living corpuscle the two are intimately mingled throughout it, and so long as this is the case the blood is opaque; but when the coloring matter dissolves in the plasma, then the blood becomes transparent, or, as it is called, *laky*. The difference may be very well seen by comparing a thin layer of fresh blood diluted with ten times its volume of ten per cent salt solution with a similar layer of blood diluted with ten volumes of water. The watery mixture is a dark transparent red; the other, in which the coloring matter still lies in the corpuscles, is a brighter opaque red.

Mature human red corpuscles do not possess nuclei; they are not, therefore, living cells in the ordinary sense. Whether they contain any living protoplasm cannot be told certainly. So far as we can judge their activities they are purely mechanical and do not require the participation of living substance. In many lower animals, and after hemorrhage in man, nucleated corpuscles are present. Our ordinary non-nucleated corpuscles had them at one stage and have lost them; whether they have also lost all living protoplasm is the question we cannot answer.

Consistency. Each red corpuscle is a soft jelly-like mass which can be readily pressed out of shape. Unless the pressure be such as to rupture it, the corpuscle immediately reassumes its proper form when the external force is removed. The corpuscles are, then, highly elastic; they frequently can be seen much dragged out of shape inside the vessels when the circulation of the blood is watched in a living animal (Chap. XX), but immediately springing back to their normal form when they get a chance.

Composition. In the fresh moist state there are in 100 parts of red corpuscles 57 to 64 of water and 36 to 43 of solids. Of the solids nearly ninety per cent is hemoglobin, about one per cent inorganic salts, chiefly phosphates and chlorides of potassium, the residue the proteins and other materials of the stroma.

Number. There is considerable variation in the number of red corpuscles in any given volume of the blood. The average for the adult male is stated at 5,000,000 per cubic millimeter ($\frac{1}{155,000}$ cubic inch); for the adult female the figure is 4,500,000. The method of determining this number is to draw from the ear or finger tip an accurately measured volume of blood; this is diluted to a known volume and the number of corpuscles in a known amount of this diluted blood is counted under the microscope. From this the total number in any volume of undiluted blood can easily be calculated.

It must be remembered that the liquid part of the blood is subject to changes of volume, either in the way of increase as liquid is received into it from the digestive tract, or decrease as liquid passes from it into the tissue spaces; therefore a variation in the number of red corpuscles per cubic millimeter does not necessarily mean a corresponding variation in the total number in the Body.

Hemoglobin. This substance, which is a compound of a pigment with a protein (see Chap. I), is the functionally important part of the red corpuscle, the stroma serving merely as a framework upon which it is carried. Its importance lies in the fact that it is the main agency for the transport of the respiratory gases, oxygen and carbon dioxid (see Respiration). Its oxygen-carrying property seems to be associated with the presence of iron in the pigment portion of the hemoglobin molecule.

In the adult male about fourteen parts in the hundred by weight of the blood are hemoglobin. It has been estimated that

a man weighing 70 kilograms (154 lbs.) has in his blood about 800 grams (1.8 lbs.) of hemoglobin, which is distributed among some 30,000,000,000,000 red corpuscles, giving a superficial area of about 3,700 sq. meters (4,400 sq. yds.). On account of the very rapid circulation of the blood (see Circulation) practically the whole of this great area of hemoglobin is poured through the lungs every minute, so it is apparent that we have here a remarkably efficient arrangement for supplying the Body with oxygen and carrying off carbon dioxid.

There is a pathological condition known as *anemia* in which there is a considerable reduction in the number of red corpuscles. This is often accompanied by a diminution in the amount of hemoglobin contained in each corpuscle, so that as a result there is a serious shortage in the hemoglobin content of the Body. Persons suffering from this condition usually have little or no color, and because the oxygen-carrying mechanism of the Body is below normal there is a loss of bodily strength and endurance. The condition is more common between the ages of twelve and twenty years than at other periods, and in girls than in boys. It is not always easily overcome and should have the care of a physician. An outdoor life and plenty of nourishing food, in which iron-containing substances are included, are beneficial in such cases.

Origin and Fate of the Red Corpuscles. Mammalian red corpuscles are cells which have lost their nuclei. In the red marrow of certain bones is the so-called *hematopoietic* (corpuscle-forming) tissue where red corpuscles are constantly being formed. The cells of this corpuscle-forming tissue are continually multiplying by mitotic division (see Chap. XXXIV) and the daughter cells thus formed store up within themselves hemoglobin, lose their nuclei, either by disintegration or extrusion, and are cast off into the blood stream. It is not known how rapidly they are formed, nor how long any individual corpuscle remains actively at work in the blood stream; but it is known that sooner or later the red corpuscles become worn out, and disintegrate; the hemoglobin is decomposed in the liver or spleen in such fashion as to save the iron, and the residue is converted into the bile pigments and excreted (see Chap. XXXI).

After hemorrhage or as the result of certain pathological conditions the rate of production of red corpuscles may be much

increased. When this occurs some corpuscles are liberated into the blood stream in an immature condition, and so the blood will be found at such times to contain nucleated as well as non-nucleated red corpuscles.

In the human embryo the labor of making red corpuscles is shared by many of the organs of the Body, notably the liver and spleen.

"Laking" the Blood; Hemolysis. If by any means the red corpuscles are destroyed their contained hemoglobin is set free in solution in the plasma. Blood in which this has happened is said to be "laky," and the process is "laking," or technically *hemolysis* (blood disintegration). Laked blood is transparent, whereas whole blood is opaque. The difference depends on the fact that the intact corpuscles interrupt light rays to a much greater extent than do molecules of dissolved hemoglobin. Laked blood is not efficient enough as a carrier of respiratory gases to meet the requirements of the organism. Consequently an animal whose blood had been thus altered would die of suffocation. Blood may be laked by diluting with water, by alternate freezing and thawing, by adding ether or chloroform, and by various other treatments, noteworthy among which is the addition of specific antibodies (see p. 325).

The Colorless Blood-Corpuscles or Nucleated Blood-Cells (Fig. 99). The *colorless* or *white corpuscles* of the blood are far less

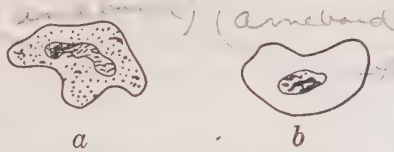


FIG. 99.—Colorless corpuscles. *a*, leucocytes proper; *b*, monocytes; *c*, lymphocytes.

numerous than the red; in health there are on the average about 5,000 to 7,000 in each cubic millimeter, but the proportion may vary considerably. Each is finely granular and consists of a soft mass of protoplasm containing a nucleus. The granules in the protoplasm commonly hide the nucleus in a fresh corpuscle, but dilute acetic acid dissolves most of them and brings the nucleus into view.

In microscopic appearance a living colorless corpuscle does not differ strikingly from such a simple one-celled organism as

Amœba. Two of the three types described below have the power of slowly changing their form spontaneously. At one moment one of them will be seen as a spheroidal mass; a few seconds later (Fig. 100) processes will be seen radiating from this, and soon after these processes may be retracted and others thrust out; and so the corpuscle goes on changing its shape. These slow *amœboid movements* are greatly promoted by keeping the specimen of blood at the temperature of the Body. By thrusting out a process on one side, then drawing the rest of its body up to it, and then sending out a process again on the same side, the corpuscle can slowly change its place and creep across the field of the microscope. Inside the blood vessels these corpuscles often execute similar movements; and they sometimes bore right through the capillary walls and, getting out into the spaces, creep about among the other tissues. This *migration* is especially frequent in inflamed parts, and the *pus* or "*matter*" which collects in abscesses is largely made up of white blood-corpuscles which have in this way got out of the blood vessels. The average diameter of the white corpuscles is one-third greater than that of the red.

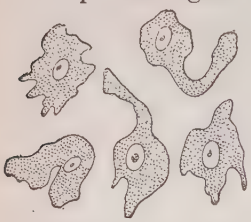


FIG. 100. — A white blood-corpuscle sketched at successive intervals of a few seconds to illustrate the changes of form due to its amœboid movements.

Under the designation colorless corpuscle are grouped at least three kinds of cells, distinct in origin, detailed structure, and function. The three kinds are named respectively, *leucocytes proper* or *microphages*, *monocytes* or *macrophages*, and *lymphocytes* (Fig. 99). The leucocytes proper are derived from antecedent cells in the red bone-marrow; they are the most numerous of the nucleated blood-cells, making up 60–75 per cent of the total of colorless corpuscles. They are capable of taking into themselves bacteria which find their way into the blood or tissue spaces; this they do in a manner similar to that in which an amœba feeds, *i. e.*, engulfing the bacteria through amœboid movements. The action was characterized by Metchnikoff as a "scavenger" action (referring to the resulting "cleansing" of the blood), and the cells which perform it as scavenger cells (*phagocytes*). The phagocytic action of leucocytes proper seems to be confined to bacteria, and the leucocytes are accordingly called microphages, to show that

their scavenger action is exerted only on minute particles. As will be shown later (p. 326) the microphages play an important rôle in the prevention and cure of infectious disease.

The second group of colorless corpuscles, the monocytes, are relatively few in number, averaging only about 300–400 per cubic millimeter of blood. They appear to be in fact nothing more nor less than characteristic cells found abundantly in the spleen and liver (see below) that have broken away and are wandering free in the blood. Like the attached cells from which they have broken free (and also like the leucocytes proper) they have the property of acting as phagocytes; but instead of engulfing bacteria they take up larger particles. When tissue damage occurs, as in cuts or bruises, monocytes collect at the point of injury and take up the cell-detritus. To distinguish them from leucocytes proper they are called macrophages (*macro* meaning large as distinct from *micro*, small). In addition to, and probably more important than their phagocytic action, the monocytes have the property of forming trephones (p. 33) and thus contributing to the growth of such cells as continue to grow and multiply in the adult. The leucocytes proper do not appear to share this property, although the lymphocytes (see below) do.

The third group of colorless corpuscles, the lymphocytes, are three or four times as numerous as the monocytes. The individual cells are smaller, and are devoid of amœboid motion and phagocytic action. They are formed in adenoid tissue (p. 404) and set free in the lymph, whence they find their way into the blood stream. The chief function known for them is that of synthesizing trephones in common with the monocytes.

The Spleen. This large and conspicuous abdominal organ (*L*, Fig. 139) consists of an outer coating or sheath of connective tissue, part fibrous and part elastic, interspersed with smooth muscle-fibers. Projections of the sheath extend into the cavity of the organ, subdividing it into numerous spaces; these are filled with the characteristic spleen cells, known as *reticulo-endothelial* cells. Similar cells, believed to have similar functions, are also present in the relatively large blood-capillaries of the liver. The spleen has a very rich blood supply which differs from that of all other organs of the Body in that the small arteries instead of communicating with capillaries, which lead in turn into veins,

open directly into the spaces filled with reticulo-endothelial cells. These cells are bathed, therefore, directly with blood, as are also the cells of similar function in the liver, and not with tissue fluid as are all the other cells. The spleen spaces are drained by tiny veins which collect the blood into larger ones and so return it to the portal vein (p. 351) whence it passes through the liver, and so on into the general circulation.

Function of Reticulo-Endothelial Tissues. These share with the monocytes of the blood the macrophage function; in other words, they take out from the blood flowing past them any non-bacterial particles that may happen to be in it. So far as the flowing blood is concerned these tissues perform most of this work, as can be shown by injecting finely divided material into the veins of an animal and examining its body after death, when the reticulo-endothelial tissues will be found loaded with the injected substance, and the monocytes charged relatively little. Of course in the process of wound repair the monocytes have to do the work, since they are the only mobile macrophages.

An important part of the macrophage function is to take care of the worn-out red corpuscles. These break down in enormous numbers each minute; so far as can be judged at present they go to pieces in the blood stream. As the blood flows through the spleen and liver the reticulo-endothelial cells take out, apparently by amœboid engulfing, the red corpuscle fragments; the iron and the portion of the corpuscle usable for nutrition, *i. e.*, its proteins, are saved; the residue of the pigment is converted into bile pigment and excreted by the liver (p. 550).

The Blood-Platelets. These are a third kind of corpuscle which remained undiscovered for a long time after the others were known because they break up and disappear very soon after the blood is shed unless special precautions are taken to preserve them. They are smaller than the red corpuscles; in structure and composition they appear to resemble somewhat the colorless corpuscles, although they do not possess a well-marked nucleus. They are said to exhibit amœboid movements under certain conditions. The only function that is known for them is in connection with the process of blood-clotting (see p. 330). They are fairly numerous, the blood containing perhaps one-tenth as many platelets as red corpuscles. The promptness with which they disintegrate when

exposed to a foreign environment is their most marked characteristic.

The Blood-Plasma. This is a very complex liquid, containing as it does all the varied substances which are associated in the carrying out of the blood's many functions. The plasma is 90 per cent water; of the remaining 10 per cent the chief portion consists of organic compounds, mostly protein, *serum albumin*, *paraglobulin*, and *fibrinogen;* the remainder is sugar, about 0.10–0.12 per cent, and fat; the latter constituent varies greatly, being considerable after a meal rich in fats, and slight at other times. About 0.8 of 1 per cent of the plasma consists of sodium, potassium, and calcium salts, the sodium salts constituting by far the greatest part of the inorganic content. The small residue is made up mostly of the waste materials which have been received into the blood from the tissues, and which are to be got rid of in the excretory organs. The most important of these are urea, creatinine, uric acid, and similar bodies. The plasma contains also the various hormones, mentioned in a previous paragraph, and a group of substances, known as *biological reagents*, which are part of the disease-resisting mechanism. These will be considered in detail in later paragraphs.

The plasma carries in solution a certain amount of oxygen, nitrogen, and carbon dioxid, but no more than a similar amount of pure water would dissolve at the same temperature. Most of the oxygen carried by the blood is in combination with the hemoglobin of the red corpuscles; most of the carbon dioxid is in combination with sodium, forming sodium bicarbonate.

Neutrality Preservation. An important fact about blood-plasma is that because it contains a mixture of carbonic acid (carbon dioxid), which is a "weak" acid, with sodium bicarbonate; and also a mixture of phosphoric acid, another "weak" acid, with salts of the same; its reaction tends to remain near neutral, in spite of changes in the whole amount of acid present in it. This is due to a property of mixtures of weak acids with their salts (known as *buffer action*), and is therefore a necessary consequence of the presence of such mixtures in the blood. It happens, nevertheless, to be of the greatest advantage to the Body, since changes in acidity might easily do harm, and are only prevented from occurring by the presence of buffers. The latter statement

will be appreciated when we note that carbon dioxid (carbonic acid) is produced in large quantities all the time, tending to make the blood more acid; also that foods may be acid or alkaline, tending to change the reaction of the blood as they are absorbed. The buffers are themselves protected from being overwhelmed by the action of the organs of elimination in excreting excess acids or alkalies. For the most part this is the work of the lungs in eliminating carbon dioxid (see p. 448).

Summary. Practically the composition of the blood may be thus stated: It consists of (1) *plasma*, consisting of watery solutions of serum albumin, paraglobulin, fibrinogen, grape-sugar, sodium, and other salts, and extractives of which the most constant are urea, creatinine, and uric acid; (2) *red corpuscles*, containing rather more than half their weight of water, the remainder being mainly hemoglobin, other proteins, and potash salts; (3) *nucleated blood cells*, consisting of water, various proteins, glycogen, and potash salts; (4) the *platelets;* (5) gases, partly dissolved in the plasma or combined with its sodium salts, and partly combined with the hemoglobin of the red corpuscles.

Quantity of Blood. The total amount of blood in the Body is difficult of accurate determination. It is about $\frac{1}{13}$ of the whole weight of the Body, so the quantity in a man weighing 70 kilos (154 lbs.) is about 5.8 kilos (12.7 lbs.). Of this at any given moment about one-fourth would be found in the heart, lungs, and larger blood vessels; and equal quantities in the vessels of the liver, and in those of the muscles which move the skeleton; while the remaining fourth is distributed among the remaining parts of the Body.

Blood of Other Animals. In all animals with blood the white corpuscles are pretty much alike, but the red corpuscles, which with rare exceptions are found only in Vertebrates, vary considerably. In all the classes of the mammalia they are circular biconcave disks, with the exception of the camel tribe, in which they are oval. They vary in diameter from 0.02 mm. ($\frac{1}{1200}$ inch) (musk deer) to 0.011 mm. ($\frac{1}{2270}$ inch) (elephant). In the dog they are nearly the same size as those of man. In no mammals do the fully-developed red corpuscles possess a nucleus. In all other vertebrate classes the red corpuscles possess a central nucleus, and are oval, slightly biconvex disks, except in a few fishes in which

they are circular. They are largest of all in the amphibia. Those of the frog are 0.022 mm. ($\frac{1}{1100}$ inch) long and 0.015 mm. ($\frac{1}{1600}$ inch) broad.

The blood of certain crustaceans contains instead of hemoglobin a substance of similar physiological action, *hemocyanin*, which is blue instead of red, and contains copper in place of iron.

Histology and Chemistry of Lymph. Pure lymph is a colorless watery-looking liquid; examined with a microscope it is seen to contain numerous white corpuscles closely resembling those of the blood, and no doubt many are leucocytes which have migrated. For the most part, however, these are lymphocytes (see above). In many parts of the Body there are collections of a peculiar *lymphoid* or *adenoid tissue* (p. 404), sometimes in nodular masses (lymphatic glands). This tissue consists essentially of a fine network, the meshes of which are occupied with lymphocytes which frequently show signs of division. The meshes of the net work communicate with lymphatic vessels and the lymph flowing through picks up and carries off the new-formed lymphocytes.

The lymph flowing from the intestines during digestion is, as already mentioned, not colorless, but white and milky. It will be considered with the process of digestion. During fasting the lymph from the intestines is colorless, like that from other parts of the Body.

Lymph is feebly alkaline, and has a specific gravity of about 1,025. The chief chemical difference between lymph and blood-plasma is that the former contains somewhat more waste materials and less food stuffs than the latter. This is because the lymph is practically identical with tissue fluid, and the consumption of food by the cells and their production of waste keep slightly ahead of the interchange of these substances between blood and tissue fluid by the processes of filtration and dialysis. Lymph contains carbon dioxid in solution but practically no oxygen, the latter substance being taken up by the living cells as fast as it enters the tissue fluid from the blood.

CHAPTER XVIII

THE DISEASE-RESISTING FUNCTION OF THE BLOOD. BLOOD-CLOTTING

Infection. Bacteriology has taught us that we are continually surrounded by myriads of micro-organisms of various kinds. They are on the skin and mucous membranes; they are breathed in with the air and swallowed in the food and water; colonies of them flourish in the intestinal tract. Not all of them are disease-producing (pathogenic), but these are nearly always present along with the harmless varieties.

Not only are these organisms always present, but small numbers of them frequently find their way into the tissue spaces of the Body, whence they get into the blood. The entry of pathogenic organisms into the Body does not constitute infection. It is only when they gain a foothold and begin to multiply that the infection is established and the disease under way.

It is recognized that the ill effects of an infection are not due to the presence of the organisms merely, but to poisonous substances, or *toxins*, which they produce as incidents in their vital processes. Some sorts give off this poison to the blood, themselves remaining out of the blood-stream; the diphtheria organism is of this sort. Others retain the toxin within themselves, and it is only when they die and decompose that the poison is liberated.

Intact Membranes Resist Infection. In order for organisms to attack the Body they have first to get within it. So long as the skin and the lining membranes of the respiratory and digestive tracts are intact the entry of organisms is difficult, if not impossible. A prime feature in the resistance to infection, therefore, is the preservation of the membranes intact. The great danger from an ordinary cold, which in itself is usually a mild infection, is in the damage to the mucous membranes which accompanies it, and which may afford channels of entry to organisms which otherwise would not be able to gain admission. In uninjured membranes, then, we have the "first line of defense" against infection.

Relation of Cells to Foreign Proteins; Immunity. The point has already been made that different kinds of organisms differ in the exact nature of their proteins (p. 20). It follows that when an infecting organism invades the Body it brings in proteins that are "foreign" to those of which the Body itself is composed. One of the very interesting facts of Biology is that living cells react defensively against "foreign" proteins of all sorts; their reaction against pathogenic organisms, which is what concerns us just now, being a special case of this general defensive reaction.

For the benefit of the reader who may wish to pursue this matter further, the special terminology in use is introduced into the following account. First is to be noted that any "foreign" protein against which cells react defensively is known as an *antigen*. When any antigen finds its way into the tissue spaces and blood vessels of the Body, and remains there long enough to become a real part of the cell-environment, it brings about changes in the metabolism of some or all of the cells (one of the points not yet determined is whether the reaction is general or is confined to special tissues, such as the reticulo-endothelial). The change comes on gradually, requiring usually 6–10 days in man. As the result of their changed metabolism the cells affected produce and pass out into the blood definite substances known as *antibodies*. These have the property of combining with antigens in such a way as to nullify their action as factors in cell-environment.

A fact of fundamental importance in the matter is that each given antigen stimulates the cells under its influence to the formation of antibodies that will react with that antigen and no other. In other words each antibody is specific for the antigen under whose influence it is produced. This is all the more remarkable when we note that one animal produces exactly the same kind of antibody for a given antigen as another; the cells that form the antibodies may be very different, but so long as the antigen is the same these different cells will produce identical antibodies. Equally remarkable is the fact that a number of different antigens may be present in the cell-environment simultaneously and antibodies will be formed for each, so far as we can find out all being produced by the same cells at one and the same time. When we think of the possibility of superposing on the already complex metabolism of the Body-cells the additional burden of manufacturing and

pouring out a series of specific antibodies under the stimulating influence of a corresponding series of definite antigens, we are brought face to face in a particularly forcible manner with the potentialities of living protoplasm.

The act of altering the metabolism of cells through the influence of antigens is known as the process of *immunization*. The organism that has antibodies in its blood and tissue fluids as the result of immunization is said to be *immune* toward the particular antigens with which its antibodies will react.

The Antibody-Antigen Reaction and Disease Prevention. There are only a few ways in which foreign proteins can get into the blood-stream and tissue spaces. The proteins of which our food is so largely composed are disintegrated into their constituent amino acids by the process of digestion (p. 490), hence we rarely receive any from that source; by far the greater part enter in the bodies of invading micro-organisms.

Whenever the Body is thus invaded the proteins, even though inside the micro-organisms, act as antigens. The Body may already have antibodies for those particular antigens, or it may not; if it has them the regular antibody-antigen reaction takes place, resulting in the immediate destruction of the micro-organisms (see below for details of the action). If none of the specific antibodies are present the organisms become established, an infection ensues, and the Body is brought under the influence of these particular antigens long enough for immunization to occur (unless in the meantime the toxins of the disease kill the Body). It follows that we *escape from infection*, when pathogenic micro-organisms actually invade the Body, only because we happen to be in possession of the right kind of antibodies.

Natural Immunity. According to the account given above there is only one way to acquire antibodies, namely, by undergoing an invasion of the Body by the specific antigens; this implies that we cannot become immune toward any disease except by passing through an attack of it. A fact of common knowledge, however, is that most people are immune to a variety of diseases, without having previously suffered from them, so far as is known. This fact is strikingly brought out whenever races come in contact with diseases to which they have not previously been exposed. Over and over again in the history of the world whole

regions have been decimated by diseases new to them, but in other lands not regarded as scourges beyond the ordinary. A striking case of the sort is the enormous mortality said to have followed the introduction of small pox to the new world by Columbus and the explorers immediately following him.

Much study has been devoted to the problem of this so-called "natural immunity." There are several possible explanations for it. Perhaps the most obvious is that parents who are made immune by passing through infection transmit the antibody-forming trait to their offspring, thus making them also immune. Students of heredity are particularly interested in this idea, for if substantiated it is a clear case of the "inheritance of acquired characters," a doctrine of heredity once much in vogue, but now completely ruled out of court by an overwhelming mass of contrary evidence. The idea has been tested by infecting guinea pigs with definite diseases and then testing their offspring to see whether they inherit the immunity. The interesting result has been obtained that often the first generation is quite immune, perhaps the second generation slightly so, but after that no effect can be seen. The explanation is that what is transmitted is not the *power to form antibodies*, *i. e.*, true immunity, but merely some of the maternal antibodies carried over from the blood of the mother to that of the fœtus. The immunity of the offspring is thus "passive immunity," and endures only so long as the antibodies received from the mother persist.

There are types of natural immunity in which it appears impossible that either individuals or their ancestors should ever have received into their bodies the antigens toward which they are immune; the presence in the blood of one species of antibodies destructive to the red corpuscles of another is a case in point (p. 315). The only conclusion possible seems to be that it is normal for cells in the course of their metabolism to form various antibodies, quite independently of special antigen stimulation. If these antibodies happen to be specific for the antigens of given pathogenic organisms the individual will be naturally immune toward the diseases the latter cause. It is probable that many instances of immunity thought to be natural are, however, really due to mild infections in childhood, which escaped notice at the time or were forgotten.

The Duration of Immunity. Different kinds of antigens differ in the persistence of their effects after they themselves have disappeared. In some cases a single infection induces immunity that endures for a lifetime, in other words, the altered metabolism brought about by the antigen becomes the normal metabolism of the affected cells. In other cases the cells return sooner or later to their former metabolism, and cease producing the special antibodies to which temporarily incited. It is probable that the immunity induced by common colds is as short-lasting as any. Individual antibodies persist in the blood a variable time; some experiments have indicated thirty days as a rough average figure. This represents the duration of passive immunity, as contrasted with active, in which antibodies continue to be formed.

The Mechanisms of Destruction of Micro-Organisms. In the paragraphs above we have shown how the conditions may be fulfilled for the occurrence of antibody-antigen reactions when pathogenic organisms invade the Body. We have now to learn how these reactions operate to bring about the destruction of the micro-organisms, and so to prevent infection from becoming established, or to rid us of it after it has persisted for a time. It is important to note that the antibody-antigen reactions themselves are not destructive to micro-organisms; the latter are highly organized cells, containing many materials additional to the special proteins that serve as antigens. About the only *direct* effect the antibody-antigen reactions seem to have on such structures is to alter their surfaces in such a way that the cells tend to clump together. This process, known as *agglutination*, occurs characteristically whenever antigen-containing cells are exposed to their specific antibodies.

The actual *destruction* of the cells depends on the operation of one or the other of two distinct agencies present in the blood, and endowed with potencies of destruction for most kinds of cells, but unable to exercise them against any except such as have undergone a previous antibody-antigen reaction. As soon as this reaction takes place, however, quite regardless of what kind of antigen or antibody is involved, one of the destructive agencies is likely to attack the cells in which the reaction has occurred and destroy them. The first of these agencies consists of the leucocytes proper, described in the last chapter (p. 316). The fact that these are

able to engulf micro-organisms is there mentioned, but the further, and more important fact, that only such micro-organisms as have previously undergone an antibody-antigen reaction are subject to attack, at least on any considerable scale, could not be brought out until the conceptions of this chapter had been established. The second agency is a soluble constituent of blood-plasma, known as the *complement*. This attacks and disintegrates cells in which an antibody-antigen reaction has occurred, although ineffective against the same cells otherwise. So far as can be determined there is only one kind of complement, present indifferently in the blood of all higher animals. The proof of this has been obtained by taking advantage of the fact that moderate heat (60° C.) destroys complement, without injuring antibodies. The experiment consists in heating a sample of "immune" blood, *i. e.*, blood containing both antibodies and complement; after heating the blood will no longer disintegrate cells which it would formerly. If, however, some non-immune blood from any source be added to the heated blood its power to disintegrate the cells toward which it is immune is restored. This restoration cannot be due to the presence of antibodies in the added blood, since the blood selected for addition is known not to have them in it; the only possible explanation is that complements are present in the added blood and so those that were destroyed by the heating are replaced when the new blood is added. Since one sort of blood answers for this purpose as well as another the experiment furnishes the proof called for that all complements are alike.

The Neutralization of Toxin by Antitoxin. A few diseases, of which diphtheria is best known, are due to organisms that pour out toxins into the blood without themselves entering it; the micro-organism-destroying reactions are obviously helpless against these. The Body is not, however, wholly at their mercy, for the toxins are themselves antigens, stimulating the tissues to manufacture specific antibodies (known in this case as *antitoxins*). The toxin-antitoxin reaction nullifies the poisonous action of the toxins and preserves the Body from harm. The unfortunate fact is, however, that these toxins are so very poisonous that they are likely to kill the Body during the interval of six days or so required for getting antitoxin production under way. The obvious treatment is to introduce antitoxin from some other source, kept ready

at hand; the passive immunity thus conferred should suffice to neutralize the toxin as fast as formed. When, in course of time, the toxin-producing organisms reach the end of their development and die the disease is over, and the patient escapes a long series of pernicious after effects commonly seen when the disease is allowed to run its course and the Body is subjected to the deleterious action of the toxin during the days while immunity is developing.

The method of obtaining antitoxin for use in passive immunization is as follows: Animals, usually horses, receive doses of toxin obtained by growing the bacteria on culture media in proper vessels. These doses are small at first, but are gradually increased as the animal acquires immunity. In course of time the blood of an animal so treated contains large quantities of antitoxin. Considerable amounts of blood can be withdrawn from animals the size of horses without their suffering the slightest inconvenience. It is thus possible to obtain abundant supplies of antitoxin.

The methods of purifying antitoxin-containing solutions are so perfect at the present time that no one should feel the least hesitation at the prospect of its use. The percentage of deaths from diphtheria has fallen from more than fifty to less than two since its introduction.

Protective Inoculation. It has been found practicable in some diseases, notably smallpox, to develop immunity by infecting the Body with an organism which is not virulent enough to endanger life but which produces antibodies that protect the Body against the more virulent infection. On account of the specific character of immunity this method can only be used where virtually the same organism occurs in virulent and nonvirulent forms.

A very hopeful path of progress toward the mastery of infectious disease is along the lines here indicated. We may look forward confidently to a time when most if not all the acute infections will be brought under medical control through application of the principles of immunity.

Carriers. A fact of interest, as well as of great moment in the problem of caring for the public health, is that an occasional infected individual, instead of destroying the invading organisms, becomes so adapted to them that he continues to live with his Body swarming with pathogenic organisms. Such a person is known as a *carrier*. He is a constant source of danger, since the organisms

he carries, and by which he is unaffected, are liable to be transferred to some susceptible individual and cause severe illness or even a widespread epidemic.

Anaphylaxis. The antibody-antigen reactions described thus far take place in the blood-stream. The antibodies are, however, formed by tissue cells from which they pass into the blood. Moreover, there is evidence that antibodies may migrate back from the blood-stream into the tissues, so that even though it may prove to be true that only certain definite tissues produce them (p. 323) they are to be found in most, if not all, tissue cells, when present anywhere in the Body. Ordinarily antibody-antigen reactions take place wholly in the blood, simply because antibodies are abundant there, and the antigens necessarily enter the blood-stream before they can reach the tissues. It may happen, however, that antibodies are not abundant enough in the blood to combine with all the antigen that presents itself; this usually means that the stimulus to immunization in the first place was not very effective, so that the cells reacted only moderately, and failed to produce a full quota of antibodies. Whenever more antigen is presented than the antibodies in the blood can take up the excess enters the tissue cells and reacts with such antibodies as are there present. In some species of animals, notably guinea pigs and dogs, and some but not nearly all human beings, the occurrence of an antibody-antigen reaction within the tissue cells results in a bodily disturbance known as *anaphylactic shock*. The disturbance is often violent, sometimes fatal. The tissues which are most markedly affected are the involuntary muscles, and death, when it occurs, is the result of cardiac or bronchial spasms, or other smooth-muscle involvements. This state of sensitiveness to particular antigens constitutes *anaphylaxis*.

Anaphylaxis is of practical importance because the administration of antitoxin involves the introduction of foreign proteins into the system, and if sensitization should take place, a second dose would have serious, or even fatal consequences. The serum (see next paragraph) of horses forms the basis of diphtheria antitoxin. Sometimes persons who are much about horses develop the condition (known as horse asthma), apparently from inhaling the protein-containing effluvium from the animals. Such persons cannot endure injections of antitoxin. They often suffer disagreeable

bronchial disturbances from the mere presence of horses. *Hay fever* is a similar sensitization toward the proteins contained in the pollen grains of plants. Ordinary *asthma* is probably another sensitization of the same sort, although the source and nature of the protein that acts as antigen is obscure. The smooth muscles of the bronchial tubes are innervated by the autonomic nervous system (p. 205), and the effect of the sympathetic subdivision on them is inhibitory; consequently they relax when nerve impulses through this channel reach them. The hormone adrenin duplicates the effects of sympathetic stimulation (p. 213), consequently relief from the bronchial spasms of hay fever and asthma can be obtained by means of adrenin. The action is palliative merely; the hormone has no effect on the underlying anaphylactic reactions.

The Coagulation of Blood. When blood is first drawn from the living Body it is perfectly liquid, flowing in any direction almost as readily as water. This condition is, however, only temporary; in a few minutes the blood becomes viscid and sticky, and the viscidity becomes more and more marked until, after the lapse of five minutes or so, the whole mass sets into a jelly which adheres to the vessel containing it, so that this may be inverted without any blood whatever being spilled. This stage is known as that of *gelatinization* and is also not permanent. In a few minutes the top of the jelly-like mass will be seen to be hollowed or "cupped" and in the concavity will be seen a small quantity of nearly colorless liquid, the *blood-serum*. The jelly next shrinks so as to pull itself loose from the sides and bottom of the vessel containing it, and as it shrinks squeezes out more and more serum. Ultimately we get a solid *clot*, colored red and smaller in size than the vessel in which the blood coagulated though retaining its form, floating in a quantity of pale yellow *serum*. If, however, the blood be not allowed to coagulate in perfect rest, a certain number of red corpuscles will be rubbed out of the clot into the serum and the latter will be more or less reddish. The longer the clot is kept the more serum will be obtained: if the first quantity exuded be decanted off and the clot put aside and protected from evaporation, it will in a short time be found to have shrunk to a smaller size and to have pressed out more serum; and this goes on until putrefactive changes commence.

Cause of Coagulation. If a drop of fresh-drawn blood be spread out very thin and watched for a few minutes with a microscope magnifying 600 or 700 diameters, it will be seen that the coagulation is due to the separation of very fine solid threads which run in every direction through the plasma and form a close network entangling all the corpuscles. These threads are composed of the protein substance *fibrin*. When they first form, the whole drop is much like a sponge soaked full of water (represented by the serum) and having solid bodies (the corpuscles) in its cavities. After the fibrin threads have been formed they tend to shorten; hence when blood clots in mass in a vessel, the fibrinous network tends to shrink in every direction just as a network formed of stretched rubber bands would, and this shrinkage is greater the longer the clotted blood is kept. At first the threads stick too firmly to the bottom and sides of the vessel to be pulled away, and thus the first sign of the contraction of the fibrin is seen in the cupping of the surface of the gelatinized blood where the threads have no solid attachment, and there the contracting mass presses out from its meshes the first drops of serum. Finally the contraction of the fibrin overcomes its adhesion to the vessel and the clot pulls itself loose on all sides, pressing out more and more serum, in which it ultimately floats. The great majority of the red corpuscles are held back in the meshes of the fibrin, but a good many leucocytes, by their amœboid movements, work their way out and get into the serum.

Whipped Blood. The essential point in coagulation being the formation of fibrin in the plasma, and blood only forming a certain amount of fibrin, if this be removed as fast as it forms the remaining blood will not clot. The fibrin may be separated by what is known as "whipping" the blood. For this purpose fresh-drawn blood is stirred up vigorously with a bunch of twigs, and to these the sticky fibrin threads as they form, adhere. If the twigs be withdrawn after a few minutes a quantity of stringy material will be found attached to them. This is at first colored red by adhering blood-corpuscles: but by washing in water they may be removed, and the pure fibrin thus obtained is perfectly white and in the form of highly elastic threads. It is insoluble in water and in dilute acids, but swells up to a transparent jelly in the latter. The "whipped" or "defibrinated blood" from which

the fibrin has been in this way removed, looks just like ordinary blood, but has lost the power of coagulating spontaneously.

Uses of Coagulation. The clotting of the blood is so important a process that its cause has been frequently investigated; but it is not yet completely understood. The living circulating blood in the healthy blood vessels does not clot; it contains no solid fibrin, but this forms in it, sooner or later, when the blood gets by any means out of the vessels or when the lining of these is injured. In this way the mouths of the small vessels opened in a cut are clogged up, and the bleeding, which would otherwise go on indefinitely, is stopped. So, too, when a surgeon ties up an artery before dividing it, the tight ligature crushes or tears its delicate inner surface, and the blood clots where that is injured, and from there a coagulum is formed reaching up to the next highest branch of the vessel. This becomes more and more solid, and by the time the ligature is removed has formed a firm plug in the cut end of the artery, which greatly diminishes the risk of bleeding.

The Source of Blood-Fibrin. Since fresh blood-plasma contains no fibrin but does contain considerable quantities of other proteins, we look first to these as a possible source of the fibrin formed during coagulation. If blood be drawn directly from the veins of a living animal by means of an oiled or waxed syringe, and be transferred at once to a cold vessel and kept just above freezing temperature it does not clot at once, so that after a time the corpuscles settle to the bottom leaving a supernatant portion of clear plasma. This plasma retains the power of clotting, as is shown when it is warmed; but if before it clots it be saturated with sodium chlorid and filtered, the liquid that remains will no longer clot. The precipitate formed by the saturation with sodium chlorid must contain, therefore, some essential in the process of clotting. This precipitate if examined will be found to be a mixture containing all the fibrinogen of the plasma and part of the globulin. These two substances may be separated by proper treatment, and after this has been done it is found that a solution of the fibrinogen can be made to clot, while one containing only paraglobulin cannot. During the clotting of the fibrinogen solution the fibrinogen disappears, giving place to fibrin.

We are thus led to the conclusion that the natural clotting of fresh blood is due to the formation of fibrin from fibrinogen which

existed in solution in the plasma of the circulating blood and has been altered in the clotted, giving origin to fibrin. But as normal blood circulating in healthy uninjured blood vessels does not clot nor do pure solutions of fibrinogen, we have still to seek the exciting cause of the change.

If to a solution of fibrinogen there be added a few drops of blood or of blood-serum, or of the washings of a blood-clot, fibrin will be formed; therefore drawn blood and serum and natural clot each contain something which can effect the conversion of fibrinogen into fibrin. This substance is *thrombin.*

Thrombin. When blood-serum is treated with several times its volume of strong alcohol its various proteins and most of its salts are precipitated: if the precipitate be left standing in alcohol for some days the proteins become almost entirely insoluble in water, but a few drops of the watery extract cause clotting in a saline solution of fibrinogen, and clearly contain some of the thrombin. This substance was for a long time believed to be an enzym or ferment (p. 489), hence the name formerly given it of "fibrin ferment." Recent careful study shows, however, that it does not correspond to enzyms in either of two cardinal characteristics, namely, the ability of a small amount of the substance to catalyze a very large amount of chemical activity, and the destruction of the substance by heating above 60° C. It has been definitely proved that the amount of fibrinogen that is converted to fibrin bears a direct relationship to the amount of thrombin present and that thrombin solutions free from protein impurities can be boiled without destroying the thrombin.

Source of Thrombin. If fresh blood is drawn directly from the veins of an animal into strong alcohol, and the resulting precipitate treated as described above for preparing thrombin from serum, it yields no thrombin; this substance, therefore, which is present in blood-serum, is absent from the blood within the Body and must be formed after the blood is shed and before the formation of the clot. We have to look, therefore, still further back, to find a precursor of thrombin. A substance has been found in fresh plasma which answers the description. It is known as *prothrombin,* to indicate its nature as thrombin precursor. When this substance is allowed to unite with calcium thrombin is formed. The latter appears to be, therefore, a prothrombin-calcium compound. Since

blood contains calcium salts as well as prothrombin nothing is lacking that enters into the composition of thrombin.

Prevention of Clotting. A fact that is bound to attract our attention is that although the blood in the vessels contains everything needed to form a clot: prothrombin and calcium which unite to form thrombin, and fibrinogen which unites with thrombin to form insoluble fibrin, it nevertheless remains unclotted. Evidently there are other agencies operating in the blood in the vessels to prevent the above reactions from taking place. Since shed blood clots these agencies must be nullified somehow in the process of shedding.

Two substances antagonistic to clotting have been found in fresh blood; one is formed in the liver, and is known as *heparin;* the second is a derivative of the first, and is designated *antithrombin.* Both are normally present in the blood in the vessels, but not in large amounts. The action of heparin is to prevent prothrombin from combining with calcium to form thrombin; the action of antithrombin is to prevent fibrinogen from reacting with thrombin to form fibrin. It is clear that the combined action of these anticoagulants should suffice to keep the blood from clotting under all ordinary conditions. This they do, as a matter of fact, and so effectively that intravascular clotting (clotting within blood vessels) is among the rarest of accidents. This is a fortunate circumstance since if clots do form they are very likely to be carried to positions where they plug important or even vitally essential vessels.

Nullification of the Anticoagulants. The final phase of the clotting mechanism is the setting free of the coagulation reactions described above by nullification of the action of heparin and antithrombin. As already pointed out, this nullification occurs whenever the blood is shed or the walls of the blood vessels injured. Moreover if the blood is allowed to come in contact with body tissues other than those to which it is regularly exposed the nullification takes place more promptly than if care is taken to protect the blood from such contact while it is being drawn (p. 338). In the tissues has been found a substance (*cephalin*) which by some means not yet determined renders the heparin ineffective. Whenever blood comes into contact with tissues the cephalin contained therein acts upon the heparin, nullifying its anticoagulating power; the prothrombin accordingly reacts with calcium forming thrombin. A portion of the thrombin thus formed

combines with the antithrombin present in the blood, giving rise to a new compound, *metathrombin*, which has no anticoagulating property. Thus the antithrombin is nullified in turn, and the second reaction of clotting, that between the remaining thrombin and fibrinogen to form fibrin, is free to proceed.

Rôle of Blood-Platelets. The process as described above takes about five to seven minutes ordinarily in man. If the blood is drawn directly from a vein, with care to prevent contact with tissues, the clotting is considerably delayed, but occurs nevertheless in all animals whose blood contains platelets; in forms without platelets, notably birds and fishes, blood thus drawn will not clot at all. This interesting fact has attracted attention ever since the platelets were discovered. Furthermore, when the process of clotting is watched under the microscope the fibrin threads will usually be seen to form about certain centers. These centers consist of disintegrating blood-platelets, and the observation that fibrin formation proceeds from them in this fashion led to the idea that the blood-platelets are in some way associated with the process.

The explanation appears to be that the platelets contain cephalin within their structure, which is set free when they disintegrate. Thus even though no tissue contact is made, and no cephalin received from that source, nullification of heparin occurs, releasing the clotting process. There is some evidence that platelets contain prothrombin as well as cephalin, so that their disintegration augments also the supply of that substance. This conception of platelet action is strengthened by the observation that any procedure which delays the disintegration of platelets delays correspondingly the clotting of blood, particularly when the latter is drawn in such manner as to avoid tissue contact. A method of preventing the platelets from disintegrating is to draw the blood through a syringe needle that has been oiled on the inside into a vessel similarly treated. If the blood does not come into contact with any surfaces which it wets the platelets remain intact for a considerable time, and clotting is postponed accordingly. This fact is taken advantage of in blood-transfusion (p. 337).

Summary of Coagulation. We may picture the entire process of blood-clotting somewhat as follows:

1. As the result of rupture of the blood vessels and contact of the blood with extraneous tissue surfaces; also as the result of

disintegration of blood-platelets, cephalin enters the blood and nullifies the anticoagulant effect of heparin.

2. Upon the nullification of heparin action prothrombin is free to combine with calcium to form thrombin, and does so.

3. Part of the thrombin formed by reaction (2) combines with the antithrombin present, to form metathrombin, a compound devoid of anticoagulant action.

4. The remainder of the thrombin reacts with fibrinogen, forming insoluble fibrin, which is precipitated as a sticky meshwork.

5. The fibrin meshwork entangles corpuscles within it, forming a typical clot.

Methods of Hastening or Retarding Coagulation. Since the process of clotting is in several steps there are a corresponding number of points at which its normal course may be broken into, either with the effect of hastening the result or of retarding it or even preventing it altogether. Anything which quickens the disintegration of the blood-platelets, as the application of a handkerchief to a wound, which acts by increasing the foreign surface in contact with the blood, makes the blood clot more quickly. The application of heat has the same effect; probably it acts both by increasing the rate of destruction of blood-platelets and by hastening the chemical reactions involved in the process as a whole. Cold, as would be expected, has the converse effect. An increase in the calcium content of the blood shortens the coagulation time. Coagulation may be retarded, as we have seen, by cold. If fresh blood is treated with any precipitant of calcium, sodium oxalate for example, the lime salts are removed and the reaction between prothrombin and calcium prevented. Clotting is thus completely prevented. Such blood will clot promptly if an excess of a soluble lime salt is added to it.

There is always a supply of heparin in storage in the liver. Intravenous injection of peptone solution causes this to be poured out into the blood in such amounts that the total cephalin brought in by tissue contact and platelet disintegration together is insufficient to nullify it. Accordingly so-called "peptone blood" will not clot. The salivary glands of leeches secrete antithrombin in concentrated form. When an extract of these glands (the purified product is called *hirudin*) is injected into the circulation of an animal or added to its blood at the moment of drawing, clot-

ting is prevented. Blood drawn into a strong solution of sodium or magnesium sulphate and well mixed will not clot, these salts appearing to interfere in some way with the formation of the thrombin; such "salted" blood will clot if thrombin is added or if diluted sufficiently with water.

An interesting fact, recently established, is that an increase in the amount of adrenin (p. 213) in the blood hastens its coagulation. This result cannot be secured by adding the hormone to the blood as it is drawn, but only by introducing it into the circulation; showing that the quickening of the clotting process is not a direct result of the chemical action of adrenin on the blood, but is brought about indirectly through the influence of the adrenin on some of the tissues through which the blood circulates. This property of adrenin is looked upon as a phase of its general function as an emergency hormone, for in time of stress and possible bodily injury prompt coagulation of the blood would tend to stop a hemorrhage quickly and so conserve the precious liquid.

"Bleeders." There is a pathological condition, fortunately not very common, known as *hemophilia*, in which the blood will not clot. Persons suffering from this disease are called *bleeders*. Such persons are in danger of bleeding to death from slight wounds; a nosebleed, or the bleeding which follows the extraction of a tooth, becomes in such persons an affair of the utmost gravity. Various explanations have been offered to account for this disease; but at present its nature remains obscure.

The condition is hereditary and behaves as a sex-linked character (p. 611). The result is that whereas the disease itself appears only in males, its transmission is through the female offspring; a father who was a "bleeder" would have no children suffering from the condition nor would his sons, but if his daughters had sons they would probably be bleeders.

Blood Transfusion. The restoration of blood lost in severe hemorrhage, or the replacement of diseased blood by healthy blood through transfusion from the veins of one individual to those of another has long been a dream of physicians and physiologists. The early attempts to treat disease by this method were more often fatal than not because the blood to be introduced into the circulation had to be defibrinated. This process, as we have seen, preserves the blood in a liquid condition, but it leaves in it

large quantities of thrombin together with excess of cephalin. When such blood was introduced into the circulation it often induced prompt clotting of the blood already there, with immediately fatal results. The fuller knowledge of the mechanism of blood-clotting gained of late years has made it clear that blood transfusion need not be followed by clotting if the transfer of blood be made without exposing it at any time to a foreign surface, such as favors the disintegration of the blood-platelets. In accordance with this idea an ingenious method was developed whereby a vessel of one individual could be brought into direct communication with a vein of another and the blood allowed to flow naturally across the living channel thus formed. More recently, in fact during the Great War, when thousands of cases calling for transfusion presented themselves in military hospitals, it was found that the discomfort and danger attending direct blood-vessel union need not be required. If care was taken to have the surfaces of all syringe needles and receiving vessels thoroughly oiled or paraffined, so that disintegration of platelets would not soon occur, or if a small amount of sodium citrate (a precipitant of calcium) was put into the syringe, the blood could be drawn directly from the veins of a donor, if necessary set aside for a few minutes, and then injected directly into the vessels of the patient, with no danger of clotting and no great discomfort to either donor or recipient.

On account of the presence in many kinds of animals of natural antibodies specific for red corpuscles of other species (p. 325), it is impractical to transfuse human patients with any other than human blood. Still more interesting and significant is the fact that not all human bloods can be mixed with impunity. Not less than four different strains exist among men, so differentiated that if the blood of a member of one strain is transfused into the vessels of a member of another antibody-antigen reactions are likely to occur. In other words, there are at least four strains among men, in which the proteins of one are "foreign" to the blood of the others in the same way as the proteins of one species are "foreign" to the blood of a quite different species. This fact makes it necessary that prospective recipients of blood by transfusion be tested to determine their strain, and only persons belonging to the same strain be selected as donors.

CHAPTER XIX

THE ANATOMY OF THE HEART AND BLOOD VESSELS

General Statement. During life the blood is kept flowing with great rapidity through all parts of the Body (except the few non-vascular tissues already mentioned) in definite paths prescribed for it by the heart and blood vessels. These paths, which under normal circumstances it never leaves, constitute a continuous set of closed tubes (Fig. 101) beginning at and ending again in the heart, and simple only close to that organ. Elsewhere it is greatly branched, the most numerous and finest branches being the *capillaries*. The heart is essentially a bag with muscular walls, internally divided into four chambers (see figure). Those at one end receive blood from vessels opening into them and known as the *veins*. From there the blood passes on to the remaining chambers which have very powerful walls and, forcibly contracting, drive the blood out into vessels which communicate with them and are known as the *arteries*. The big arteries divide into smaller; these into smaller again (Fig. 102) until the branches become too small to be traced by the unaided eye, and these smallest branches end in the *capillaries*, through which the blood flows and enters the commencements of the *veins;* and these convey it again to the heart. At certain points in the course of the blood-paths valves are placed, which prevent a back-flow. This alternating reception of blood at one end by the heart and its ejection from the other go on during life steadily about seventy times in a minute and so keep the liquid constantly in motion.

The vascular system is completely closed except at two points in the neck where lymph-vessels open into the veins; there some lymph is poured in and mixed directly with the blood. Accordingly everything which leaves the blood must do so by passing through the walls of the blood vessels, and everything which enters it must do the same, except matters conveyed in by the lymph at the points above mentioned. This interchange through the walls of

the vessels takes place only in the capillaries, which thus form a sort of irrigation system all through the Body. The heart, arteries, and veins are all merely arrangements for keeping the capillaries full and renewing the blood within them. It is in the capillaries alone that the blood does its physiological work.

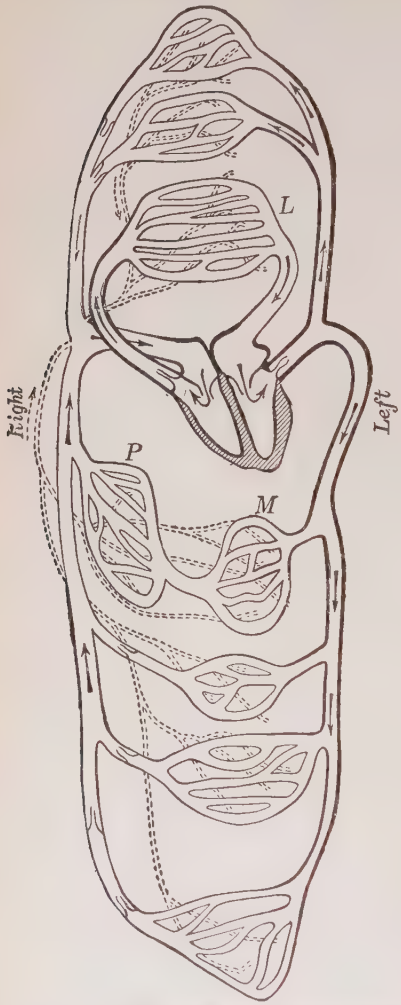


FIG. 101.—The heart and blood-vessels diagrammatically represented. *L*, lung; *M*, intestine; *P*, liver; dotted lines represent lymphatic vessels.

The Position of the Heart. The heart (*h*, Fig. 1) lies in the chest immediately above the diaphragm and opposite the lower two-thirds of the breast-bone. It is conical in form with its *base* or broader end turned upwards and projecting a little on the right of the sternum, while its narrow end or apex, turned downwards, projects to the left of that bone, where it may be felt beating between the cartilages of the fifth and sixth ribs. The position of the organ in the Body is therefore oblique with reference to its long axis. It does not, however, lie on the left side as is so commonly supposed but very nearly in the middle line, with the upper part inclined to the right, and the lower (which may be more easily felt beating—hence the common belief) to the left.

The Membranes of the Heart. The heart does not lie bare in the chest but is surrounded by a loose bag composed of connective tissue and called the *pericardium*. This bag, like the heart,

is conical but turned the other way, its broad part being lowest and attached to the upper surface of the diaphragm. Internally it is lined by a smooth *serous membrane* like that lining the abdominal cavity, and a similar layer (the *visceral layer* of the pericardium) covers the outside of the heart itself, adhering closely to it. Each

FIG. 102.—The arteries of the hand, showing the communications or anastomoses of different arteries and the fine terminal twigs given off from the larger trunks; these twigs end in the capillaries which would only become visible if magnified. *R*, the *radial artery* on which the pulse is usually felt at the wrist; *U*, the ulnar artery.

of the serous layers is covered by a stratum of flat cells, and in the space between them is found a small quantity of liquid which moistens the contiguous surfaces, and diminishes the friction which would otherwise occur during the movement of the heart.

Internally the heart is also lined by a fibrous membrane, covered with a single layer of flattened cells, and called the *endocardium*.

Between the endocardium and the visceral layer of the pericardium the bulk of the wall of the heart lies and is made up mainly of the special cardiac muscular tissue previously described (p. 95); but connective tissues, blood vessels, nerve-cells, and nerve-fibers are also abundant in it.

The Cavities of the Heart. On opening the heart (see diagram, Fig. 103) it is found to be subdivided by a longitudinal partition or *septum* into completely separated right and left halves, the partition running from about the middle of the base to a point a little on the right of the apex. Each of the chambers on the sides of the septum is again incompletely divided transversely, into a thinner basal portion into which veins open, known as the *atrium* or *auricle*, and a thicker apical portion from which arteries arise, called the *ventricle*. The heart thus consists of a right auricle and ventricle and a left auricle and ventricle, each auricle communicating by an *auriculoventricular orifice* with the ventricle on its own side, and there is no direct communication whatever through the septum between the opposite sides of the heart. To get from one side to the other the blood must leave the heart and pass through a set of capillaries, as may readily be seen by tracing the course of the vessels in Fig. 101.

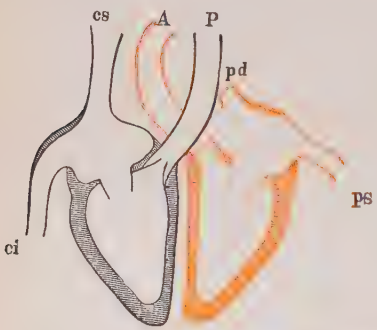


Fig. 103.—Diagram representing a section through the heart from base to apex.

The Heart as Seen from its Exterior. When the heart is viewed from the side turned towards the sternum (Fig. 104) the two auricles, *Atd* and *As*, are seen to be separated by a deep groove from the ventricles, *Vd* and *Vs*. A more shallow furrow runs between the ventricles and indicates the position of the internal longitudinal septum. On the dorsal aspect of the heart (Fig. 105) similar furrows may be noted, and on one or other of the two figures the great vessels opening into the cavities of the heart may be seen. The *pulmonary artery*, *P*, arises from the right ventricle, and very soon divides into the right and left pulmonary arteries, *Pd* and *Ps*, which break up into smaller branches and enter the

corresponding lungs. Opening into the right auricle are two great veins (see also Fig. 103), *cs* and *ci*, known respectively as the *superior* and *inferior venæ cavæ*, or "hollow" veins; so called by the older anatomists because they are frequently found empty after death. Into the back of the right auricle opens also another

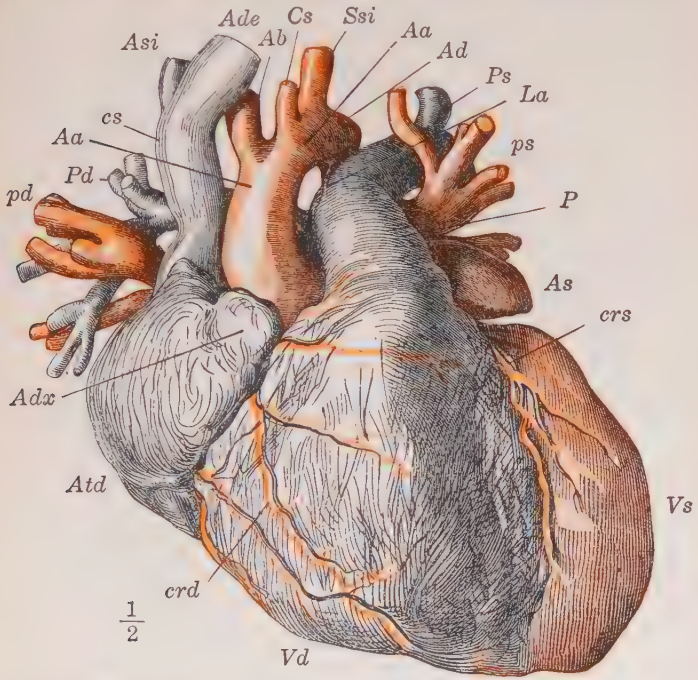


FIG. 104.—The heart and the great blood vessel attached to it, seen from the side towards the sternum. The left cavities and the vessels connected with them are colored red; the right black. *Atd*, right auricle; *Adx* and *As*, the right and left auricular appendages; *Vd*, right ventricle; *Vs*, left ventricle; *Aa*, aorta; *Ab*, innominate artery; *Cs*, left common carotid artery; *Ssi*, left subclavian artery; *P*, main trunk of the pulmonary artery, and *Pd* and *Ps*, its branches to the right and left lungs; *cs*, superior vena cava; *Ade* and *Asi*, the right and left innominate veins; *pd* and *ps*, the right and left pulmonary veins; *crd* and *crs*, the right and left coronary arteries.

vein, *Vc*, called the *coronary vein* or *sinus*, which brings back blood that has circulated in the walls of the heart itself. Springing from the left ventricle, and appearing from beneath the pulmonary artery when the heart is looked at from the ventral side, is a great artery, the *aorta*, *Aa*. It forms an arch over the base of the heart and then runs down behind it at the back of the chest. From the

convexity of the arch of the aorta several great branches are given off, *Ssi*, *Cs*, *Ab;* but before that, close to the heart, the aorta gives off two *coronary arteries*, branches of which are seen at *crd* and *crs* lying in the groove over the partition between the ventri-

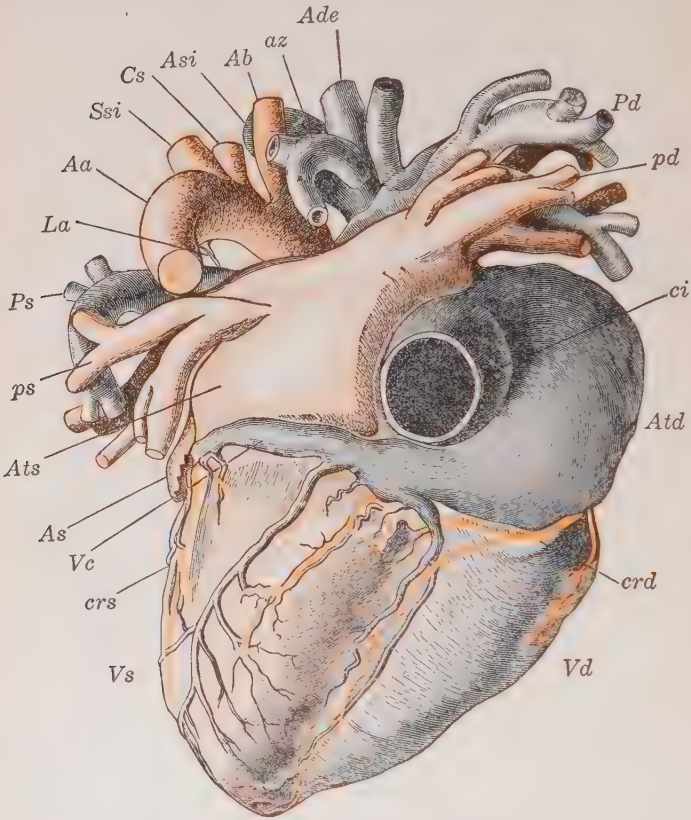


Fig. 105.—The heart viewed from its dorsal aspect. *Atd*, right auricle; *ci*, inferior vena cava; *Vc*, coronary vein. The remaining letters of reference have the same signification as in Fig. 104.

cles, and which carry to the substance of the organ that blood which comes back through the coronary sinus. Into the left auricle open two right and two left *pulmonary veins*, *ps* and *pd*, which are formed by the union of smaller veins proceeding from the lungs.

In the diagram Fig. 103, from which the branches of the great vessels near the heart have been omitted for the sake of clearness, the connection of the various vessels with the chambers of the heart can be better seen. Opening into the right auricle are the superior and inferior venæ cavæ (*cs* and *ci*) and proceeding from the right ventricle the *pulmonary artery*, *P*. Opening into the left auricle are the right and left pulmonary veins (*pd* and *ps*) and springing from the left ventricle the aorta, *A*.

The Interior of the Heart. The communication of each auricle with its ventricle is also represented in the diagram Fig. 103, and the valves which are present at those points and at the origin of the pulmonary artery and that of the aorta. Internally the auricles are for the most part smooth, but from each a hollow pouch, the *auricular appendage*, projects over the base of the corresponding ventricle as seen at *Adx* and *As* in Figs. 104 and 105. These pouches have somewhat the shape of a dog's ear and have given their name to the whole auricle. Their interior is roughened by muscular elevations, covered by endocardium, known as the fleshy columns (*columnæ carnæ*). On the inside of the ventricles (Fig. 106) similar fleshy columns are very prominent.

The Auriculoventricular Valves. These are known as *right* and *left*, or as the *tricuspid* and *mitral valves* respectively. The mitral valve (Fig. 106) consists of two flaps of the endocardium fixed by their bases to the margins of the auriculoventricular aperture and with their edges hanging down into the ventricle when the heart is empty. These unattached edges are not, however, free, but have fixed to them a number of stout connective-tissue cords, the *cordæ tendineæ*, which are fixed below to muscular elevations, the *papillary muscles*, *Mpm* and *Mpl*, on the interior of the ventricle. The cords are long enough to let the valve flaps rise into a horizontal position and so close the opening between auricle and ventricle which lies between them, and passes up behind the opened aorta, *Sp*, represented in the figure. The *tricuspid valve* is like the mitral, but with three flaps instead of two.

Semilunar Valves. These are six in number: three at the mouth of the aorta, Fig. 106, and three, quite like them, at the mouth of the pulmonary artery. Each is a strong crescentic pouch fixed by its more curved border, and with its free edge turned away from the heart. When the valves are in action these free edges

meet across the vessel and prevent blood from flowing back into the ventricle. In the middle of the free border of each valve is a little cartilaginous nodule, the *corpus Arantii*, and on each side of

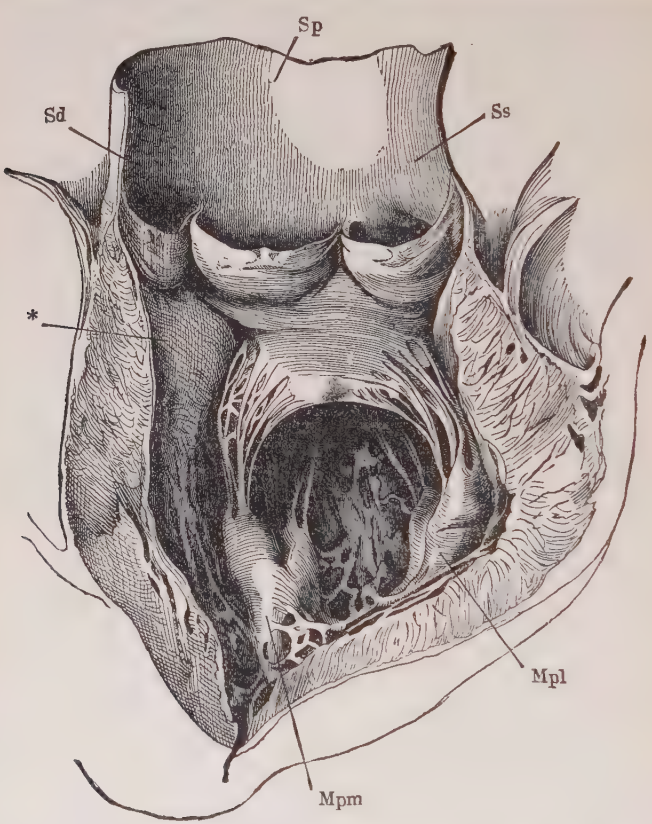


FIG. 106.—The left ventricle and the commencement of the aorta laid open. *Mpm*, *Mpl*, the papillary muscles. From their upper ends are seen the *cordæ tendineæ* proceeding to the edges of the flaps of the mitral valve. The opening into the auricle lies between these flaps. At the beginning of the aorta are seen its three pouch-like semilunar valves.

this the edge of the valve is very thin and when it meets its neighbor turns up against it and so secures the closure.

The Arterial System. All the arteries of the Body arise either directly or indirectly from the aorta or pulmonary artery, and the great majority of them from the former vessel. The pulmonary artery carries blood only to the lungs, to undergo exchanges

with the air in them after it has circulated through the Body generally.

After making its arch the aorta continues back through the chest, giving off many branches on its way. Piercing the diaphragm it enters the abdomen and after supplying the parts in and around that cavity with branches, it ends opposite the last lumbar vertebra by dividing into the *right* and *left common iliac* arteries, which carry blood to the lower limbs. We have then to consider the branches of the arch of the aorta, and those of the *descending aorta*, which latter is for convenience described by anatomists as consisting of the *thoracic aorta*, extending from the end of the arch to the diaphragm, and the *abdominal aorta*, extending from the diaphragm to the final subdivision of the vessel.

Branches of the Arch of the Aorta. From this arise first the *coronary arteries* (*crd* and *crs*, Figs. 104 and 105) which spring close to the heart, just above two of the pouches of the semilunar valve, and carry blood into the substance of that organ. The remaining branches of the arch are three in number, and all arise from its convexity. The first is the *innominate artery* (*Ab*, Fig. 104), which is very short, immediately breaking up into the *right subclavian artery*, and the *right common carotid*. Then comes the *left common carotid*, *Cs*, and finally the *left subclavian*, *Ssi*.

Each *subclavian artery* runs out to the arm on its own side and after giving off a *vertebral artery* (which runs up the neck to the head in the vertebral canal of the transverse processes of the cervical vertebræ), crosses the armpit and takes there the name of the *axillary artery*. This continues down the arm as the *brachial artery*, which, giving off branches on its way, runs to the front of the arm, and just below the elbow-joint divides into the *radial* and *ulnar arteries*, the lower ends of which are seen at *R* and *U* in Fig. 102. These supply the forearm and end in the hand by uniting to form an arch, from which branches are given off to the fingers.

The *common carotid arteries* pass out of the chest into the neck, along which they ascend on the sides of the windpipe. Opposite the angle of the lower jaw each divides into an *internal* and *external carotid artery*, right or left as the case may be. The external ends mainly in branches for the face, scalp, and salivary glands, one great subdivision of it with a tortuous course, the *temporal artery*, being often seen in thin persons beating on the side of the

brow. The internal carotid artery enters the skull through an aperture in its base and supplies the brain, which it will be remembered gets blood also through the vertebral arteries.

Branches of the Thoracic Aorta. These are numerous but small. Some, the *intercostal arteries*, run out between the ribs and supply the chest-walls; others, the *bronchial arteries*, carry blood to the lungs for their nourishment, that carried to them by the pulmonary arteries being brought there for another purpose; and a few other small branches are given to other neighboring parts.

Branches of the Abdominal Aorta. These are both large and numerous, supplying not only the wall of the posterior part of the trunk, but the important organs in the abdominal cavity. The larger are: the *celiac axis* which supplies stomach, spleen, liver, and pancreas; the *superior mesenteric artery*, which supplies a great part of the intestine; the *renal arteries*, one for each kidney; and finally the *inferior mesenteric artery*, which supplies the rest of the intestine. Besides these the abdominal aorta gives off very many smaller branches.

Arteries of the Lower Limbs. Each common iliac divides into an *internal* and *external iliac artery*. The former ends mainly in branches to parts lying in the pelvis, but the latter passes into the thighs and there takes the name of the *femoral artery*. At first this lies on the ventral aspect of the limb, but lower down passes to the back of the femur, and above the knee-joint (where it is called the *popliteal artery*) divides into the *anterior* and *posterior tibial arteries*, which supply the leg and foot.

The Capillaries. As the arteries are followed from the heart, their branches become smaller and smaller, and finally cannot be traced without the aid of a microscope. The smallest arteries are called *arterioles*. These pass into the *capillaries* (Fig. 109), the walls of which are simpler than those of the arterioles, and which form very close networks in nearly all parts of the Body; their immense number compensating for their small size. The average diameter of a capillary vessel is about 0.008 mm. ($\frac{1}{3000}$ inch) so that the blood-corpuscles must pass through it usually in single file; and in many parts they are so close that seven hundred or so are packed in a space the size of the shaft of a pin (p. 10). It is while flowing in these delicate tubes that the blood does its nutritive work, the arteries being merely supply-tubes for the capillaries.

The Veins. The first veins arise from the capillary networks and like the last arteries are very small. They soon increase in size by union, and so form larger and larger trunks. These in many places lie near or alongside the main artery of the part, but

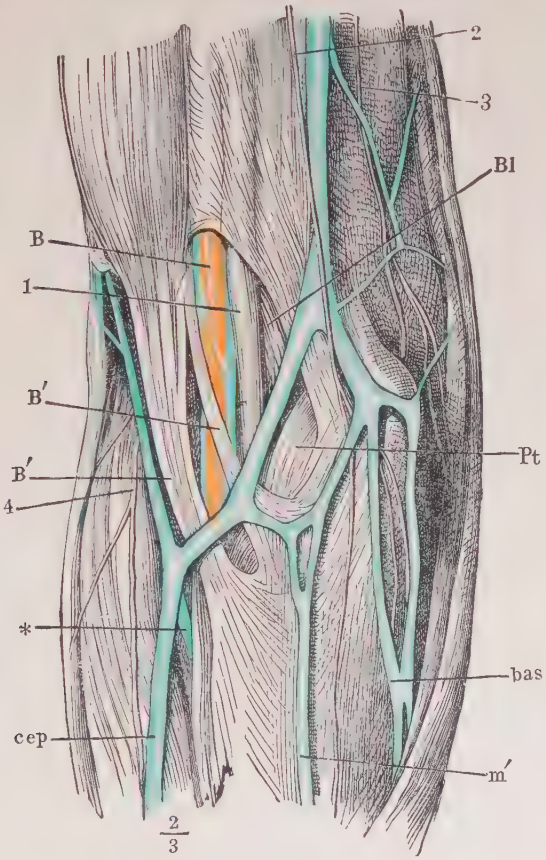


Fig. 107.—The superficial veins in front of the elbow-joint. *B′*, tendon of *biceps* muscle; *Bi*, *brachialis internus* muscle; *Pt*, *pronator teres* muscle; 1, median nerve; 2, 3, 4, nerve-branches to the skin; *B*, brachial artery, with its small accompanying veins; *cep*, cephalic vein; *bas*, basilic vein; *m′*, median vein; *, junction of a deep-lying vein with the cephalic.

there are many more large veins just beneath the skin than there are large arteries. This is especially the case in the limbs, the main veins of which are superficial, and can in many persons be seen as faint blue marks through the skin. Fig. 107 represents the arm

at the front of the elbow-joint after the skin and subcutaneous connective tissue and fat have been removed. The brachial artery, *B*, colored red, is seen lying tolerably deep, and accompanied by two small veins (*venæ comites*) which communicate by cross-branches. The great *median nerve*, 1, a branch of the brachial plexus which supplies several muscles of the forearm and hand, the skin over a great part of the palm and the three inner fingers, is seen alongside the artery. The larger veins of the part are seen to form a more superficial network, joined here and there, as for instance at *, by branches from deeper parts. Several small nerve-branches which supply the skin (2, 3, 4) are seen among these veins. It is from the vessel, *cep*, called the *cephalic vein*, just above the point where it crosses the median nerve, that surgeons usually bleed a patient.

A great part of the blood of the lower limb is brought back by the *long saphenous vein*, which can be seen in thin persons running from the inner side of the ankle to the top of the thigh. All the blood which leaves the heart by the aorta, except that flowing through the coronary arteries, is finally collected into the *superior* and *inferior venæ cavæ* (*cs* and *ci*, Figs. 104 and 105), and poured into the right auricle. The *jugular veins* which run down the neck, carrying back the blood which went out along the carotid arteries, unite below with the arm-vein (*subclavian*) to form on each side an *innominate vein* (*Asi* and *Ade*, Fig. 104) and the innominates unite to form the superior cava. The coronary-artery blood after flowing through the capillaries of the heart itself also returns to this auricle by the coronary veins and sinus.

The Pulmonary Circulation (*L*, Fig. 101). Through this the blood gets back to the left side of the heart and so into the aorta again. The pulmonary artery, dividing into branches for each lung, ends in the capillaries of those organs. From these the blood is collected by the pulmonary veins, which carry it back to the left auricle, whence it passes to the left ventricle to recommence its flow through the Body generally.

The Course of the Blood. From what has been said it is clear that the movement of the blood is a *circulation*. Starting from any one chamber of the heart it will in time return to it; but to do this it must pass through at least two sets of capillaries; one of these is connected with the aorta and the other with the pulmonary

artery, and in its circuit the blood returns to the heart twice. Leaving the left side it returns to the right, and leaving the right it returns to the left; and there is no road for it from one side of the heart to the other except through a capillary network. Moreover, it always leaves from a ventricle through an artery, and returns to an auricle through a vein.

There is then really only one circulation; but it is not uncommon to speak of two, the flow from the left side of the heart to the right, through the Body generally, being called the *systemic circulation*, and from the right to the left, through the lungs, the *pulmonary circulation*. But since after completing either of these alone the blood is not back at the point from which it started, but is separated from it by the septum of the heart, neither is a "circulation" in the proper sense of the word.

The Portal Circulation. A certain portion of the blood which leaves the left ventricle of the heart through the aorta has to pass through three sets of capillaries before it can again return there. This is the portion which goes through the stomach, spleen, pancreas, and intestines (*M*, Fig. 101). After traversing the capillaries of those organs it is collected into the *portal vein* which enters the liver, and breaking up in it into finer and finer branches like an artery, ends in the capillaries of that organ, forming the second set which this blood passes through on its course (*P*, Fig. 101). From these it is collected by the *hepatic veins*, which pour it into the inferior vena cava, which carries it to the right auricle, so that it has still to pass through the pulmonary capillaries to get back to the left side of the heart. The flow from the stomach and intestines through the liver to the vena cava is often spoken of as the *portal circulation*.

Diagram of the Circulation. Since the two halves of the heart are actually completely separated from one another by an impervious partition, although placed in proximity in the Body, we may conveniently represent the course of the blood as in the accompanying diagram (Fig. 108), in which the right and left halves of the heart are represented at different points in the vascular system. Such an arrangement makes it clear that the heart is really two pumps working side by side, each engaged in forcing the blood to the other. Starting from the left auricle, *la*, and following the flow, we trace it through the left ventricle and along

the branches of the aorta into the systemic capillaries, *sc;* from thence it passes back through the systemic veins, *vc*. Reaching the right auricle, *ra*, it is sent into the right ventricle, *rv*, and thence through the pulmonary artery, *pa*, to the lung capillaries, *pc*, from which the pulmonary veins, *pv*, carry it to the left auricle, which drives it into the left ventricle, *lv*, and this again into the aorta.

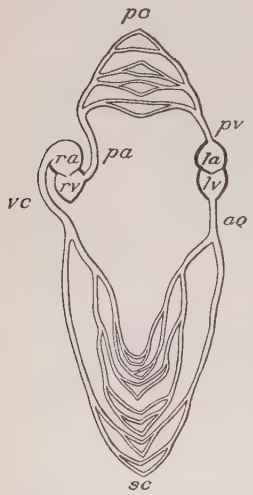


Fig. 108.—Diagram of the blood vascular system, showing that it forms a single closed circuit with two pumps in it, consisting of the right and left halves of the heart, which are represented separate in the diagram. *ra* and *rv*, right auricle and ventricle; *la* and *lv*, left auricle and ventricle; *ao*, aorta; *sc*, systemic capillaries; *vc*, venæ cavæ; *pa*, pulmonary artery; *pc*, pulmonary capillaries; *pv*, pulmonary veins.

Arterial and Venous Blood. The blood when flowing in the pulmonary capillaries gives up carbon dioxid to the air and receives oxygen from it; and since its coloring matter (hemoglobin) forms a scarlet compound with oxygen, it flows to the left auricle through the pulmonary veins of a bright red color. This color it maintains until it reaches the systemic capillaries, where it loses much oxygen to the surrounding tissues and gains much carbon dioxid from them. But the blood coloring matter which has lost its oxygen has a dark purple color, and since this "reduced" hemoglobin is now in excess, the blood returns to the heart by the venæ cavæ of a dark purple-red color. This hue it keeps until it reaches the lungs, when the reduced hemoglobin becomes again oxidized. The bright red blood, rich in oxygen and poor in carbon dioxid, is known as "arterial blood" and the dark red as "venous blood": and it must be borne in mind that the terms have this peculiar technical meaning, and that the pulmonary *veins* contain *arterial* blood, and the pulmonary *arteries*, *venous* blood; the change from arterial to venous taking place in the systemic capillaries, and from venous to arterial in the pulmonary capillaries. The chambers of the heart and the great vessels containing arterial blood are shaded red in Figs. 104 and 105.

The Structure of the Arteries. A large artery can by careful dissection be separated into three coats: an *internal*, a *middle*, and an *outer*. The internal coat tears readily across the long axis of the

artery and consists of an inner lining of flattened nucleated cells, known as the *tunica intima*, enveloped by a variable number of layers composed of membranes or networks of elastic tissue. The middle coat is made up of alternating layers of elastic fibers and plain muscular tissue; the former running for the most part longitudinally and the latter across the long axis of the vessel. The outer coat is the toughest and strongest because it is mainly made up of white fibrous connective tissue; it contains a considerable amount of elastic tissue also, and gradually shades off into a loose areolar tissue which forms the *sheath* of the artery, or the *tunica adventitia*, and packs it between surrounding parts. The smaller arteries have all the elastic elements less developed. The internal coat is consequently thinner, and the middle coat is made up mainly of smooth muscular fibers. As a result the large arteries are highly elastic, the aorta being physically much like a piece of rubber tubing, while the smaller arteries are highly contractile, in the physiological sense of the word.

Structure of the Capillaries. In the smaller arteries the outer and middle coats gradually disappear, and the elastic layers of

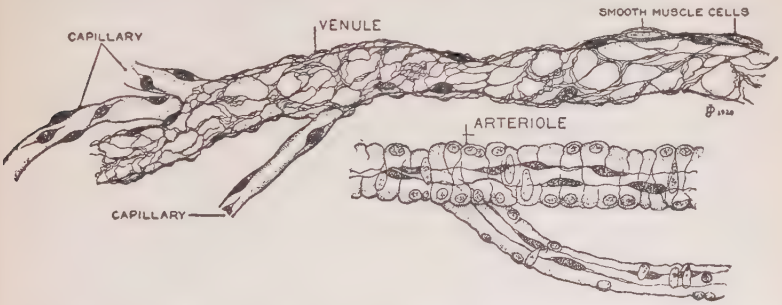


Fig. 109.—Capillaries in relation to arterioles and venules (Hooker). In these capillaries no Rouget cells are visible.

the inner coat also go. Finally in the capillaries the intima alone is left (Fig. 109), with occasional scattered cells (*Rouget* cells) to represent the last vestiges of the muscular layer here and there on its surface. These vessels are thus extremely well adapted to allow of filtration or dialysis taking place through their thin walls.

Structure of the Veins. In these the same three primary coats as in the arteries are found; the inner and middle coats are less developed, while the outer one remains thick, and is made up almost

entirely of white fibrous tissue. Hence the venous walls are much thinner than those of the corresponding arteries, and the veins collapse when empty while the stouter arteries remain open. But the toughness of their outer coats gives the veins great strength.

Except the pulmonary artery and the aorta, which possess the semilunar valves at their cardiac orifices, the arteries possess no valves. Many veins, on the contrary, have such, formed by semilunar pouches of the inner coat, attached by one margin and having the edge turned towards the heart free. These valves sometimes single, oftener in pairs, and rarely three at one level, permit blood to flow only towards the heart, for a current in that direction (as in the upper diagram, Fig. 110) presses the valve close against the side of the vessel and meets with no obstruction from it. Should any back-flow be attempted, however, the current closes up the valve and bars its own passage as indicated in the lower figure. These valves are most numerous in superficial veins and those of muscular parts. They are absent in the venæ cavæ and the portal and pulmonary veins. Usually the vein is a little dilated opposite a valve, and hence in parts where the valves are numerous gets a knotted look. On compressing the forearm so as to stop the flow in its subcutaneous veins and cause their dilation, the points at which valves are placed can be recognized by their swollen appearance. They are most frequently situated where two veins communicate.

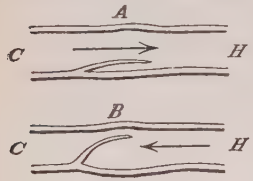


Fig. 110.—Diagram to illustrate the mode of action of the valves of the veins. *C*, the capillary end, and *H*, the heart end of the vessel.

CHAPTER XX

THE ACTION OF THE HEART. THE REGULATION OF THE HEART-BEAT

The Beat of the Heart. It is possible with some little skill and care to open the chest of a living narcotized animal, such as a rabbit, and see its heart at work, alternately contracting and relaxing. As observed under ordinary conditions these phases follow one another so rapidly as seemingly to defy analysis. When Harvey, the discoverer of the circulation, first looked upon the beating heart of a mammal he was so impressed by the complexity and rapidity of its action as to believe for the moment that the human mind could never fathom it.

By proper treatment the beat of the heart can be much slowed. When this has been done it is observed that each beat commences at the mouths of the great veins; from there runs over the rest of the auricles, and then over the ventricles; the auricles relaxing the moment the ventricles commence to contract. Having finished their contraction the ventricles also relax, and so for some time neither they nor the auricles are contracting, but the whole heart is at rest. The contraction of any part of the heart is known as its *systole* and the relaxation as its *diastole*.

The average heart-rate in man is 72 beats per minute, giving for each beat just over 0.8 second. The two sides of the heart work synchronously, the auricles together and the ventricles together. In describing the "cardiac cycle," therefore, the auricles are treated as one organ and the ventricles as one. The *auricular systole* occupies about 0.1 second, its *diastole* lasts 0.7 second. The *ventricular systole* begins at the end of the auricular contraction; it occupies about 0.3 second; the *diastole* of the ventricle lasts about 0.5 second. During fully half of each cardiac cycle, then, there is no muscular activity going on in any part of the heart. During diastole the heart if taken between the finger and thumb feels soft and flabby, but during systole it (especially its ventricular portion) becomes hard and rigid.

Change of Form of the Heart. During its systole the heart becomes shorter and rounder, mainly from a change in the shape of the ventricles, which from having an elliptical cross-section take on a circular one. At the same time the length of the ventricles is lessened, the apex of the heart approaching the base and becoming blunter and rounder.

The Cardiac Impulse. The human heart lies with its apex touching the chest-wall between the fifth and sixth ribs on the left side of the breast-bone. At every beat a sort of tap, known as the "cardiac impulse" or "apex beat," may be felt by the finger at that point. There is, however, no actual "tapping", since the heart's apex never leaves the chest-wall. During the diastole the soft ventricles yield to the chest-wall where they touch it, but during the systole they become hard and tense and push it out a little between the ribs, and so cause the apex beat. Since the heart becomes shorter during the ventricular systole, it might be supposed that at that time the apex would move up a little in the chest. This, however, is not the case, the ascent of the apex towards the base of the ventricles being compensated for by a movement of the whole heart in the opposite direction. If water be pumped into an elastic tube, already moderately full, the tube will be distended not only transversely but longitudinally. This is what happens in the aorta: when the left ventricle contracts and pumps blood forcibly into it, the elastic artery is elongated as well as widened, and the lengthening of that limb of its arch attached to the heart pushes the latter down towards the diaphragm, and compensates for the upward movement of the apex due to the shortening of the ventricles. Hence if the exposed living heart be watched it appears as if during the systole the base of the heart moved towards the tip, rather than the reverse.

Before undertaking to describe the heart's action in detail something more about its intimate structure and special physiological character will be given, in order that the account shall be clear.

Relations of Nerve and Muscle Elements within the Heart. The heart-muscle consists, as previously stated (p. 95) of muscle-cells of small size, intimately communicating with one another through their branches, and showing signs of cross-striation. At the junction of the great veins with the heart, a region, as we shall

see, of great importance in the heart's activity, these muscular elements form thin sheets; in the auricles the heart-muscle is somewhat heavier and thicker; but it attains its greatest development in the ventricles, where the muscular walls are exceedingly heavy, and very stout. In mammals the only pulsating heart structures are the auricles and ventricles; in lower vertebrates, such as the frog, the great veins near the heart are differentiated into a pulsating structure, the *sinus venosus*, and the outlet from the ventricle, the *bulbus arteriosus*, also pulsates. Although in mammals these structures no longer pulsate, the region of the great veins which corresponds to the sinus venosus still seems to preserve to some degree the physiological properties it has in lower animals, and observations made upon frogs' hearts are interpreted for mammals' hearts upon that basis.

Imbedded within the tissue of the heart are numerous nerve-cells. These are especially numerous in the region of the sinus venosus and auricles; the base of the ventricles contains some of them, but the apex of the ventricles is said to be wholly free from them. Nerve-fibers, communicating with these cells, penetrate all parts of the cardiac musculature. It has not been possible by histologic means to show that these fibers are dendrites and axons such as occur in the general nervous system, and many histologists and physiologists believe that they form a continuous network or plexus involving all parts of the heart and so constituted that a stimulus applied at any point spreads over the whole organ. According to this view the nervous mechanism of the heart is not a "synaptic system" and so does not show the irreversibility of conduction which is a cardinal feature of the general nervous system. Certain other viscera, notably the stomach and intestines, have within their walls nerve plexuses showing similar physiological properties.

Physiological Peculiarities of the Heart. The most striking of these is its *automatic rhythmicity*. The heart may be removed completely from the Body without its regular beating being at all interfered with. In cold-blooded animals such as frogs or turtles this activity outside the Body may continue for hours. While we refer to this activity as *automatic* we do not mean by the word anything more than the fact just stated, that the heart continues to beat independently of the rest of the Body. The *rhythmic* nature of the heart's activity is as characteristic as its automaticity.

The regular succession of contractions and relaxations is its normal response to continuous or rapidly recurring stimulation. In this respect it differs strikingly from skeletal muscle, which remains strongly contracted throughout the period of such stimulation unless fatigue sets in to release it.

Another peculiarity of heart-muscle, and one that probably explains in part its rhythmic property, is that its contractions are always *maximal;* in other words, whenever any of the fibers in a given chamber-wall (auricle or ventricle) contract, all do so. This results from the fact that the fibers intercommunicate with one another, as described above, so that an impulse once started spreads over the whole mass of fibers.

The additional peculiarity on which the explanation of rhythmicity rests is an apparent difference in the speed with which the restorative reactions occur following contraction. In the account of skeletal-muscle tetanus (p. 121) it is stated that the formation of the lactic acid precursor ("glucose phosphate") from glucose or glycogen is practically coincident with its using up as the result of stimulation. There is always, thus, a supply of acid-precursor available no matter how rapidly the stimuli may follow one another. In heart-muscle, in contrast, it appears that the reformation of acid-precursor is a more gradual process; consequently an interval must always elapse after one contraction before another can take place. This interval is known as the *refractory phase of cardiac contraction.* During this period, which coincides with the early part of systole, external stimulation of the heart-muscle is altogether ineffective. In late systole and throughout diastole the heart will respond to adequate stimulation. It is observed, however, that the irritability of the heart increases steadily from the end of the refractory period to the beginning of the next automatic contraction. This is taken to mean that the supply of acid-precursor is being built up during all that time, and as more accumulates the heart becomes more irritable. Since the beats of the heart are maximal, all fibers partaking in each contraction, there is no possibility that different fibers may act in rotation; thus all the properties of cardiac muscle join to insure that the heart-beat shall be rhythmical.

The Passage of the Beat over the Heart. In the first paragraph of the chapter it was stated that the beat of the heart takes a

certain course, beginning at the mouths of the great veins, spreading thence over the auricles, and passing from them to the ventricles. In all vertebrates there is a distinct pause between the contraction of the auricles and of the ventricles. In animals, such as the frog and turtle that have a pulsating sinus, there is likewise a pause between the contraction of the sinus and of the auricles.

All that is left of the sinus in mammals is a characteristic mass of cells located near the junction of the great veins with the right

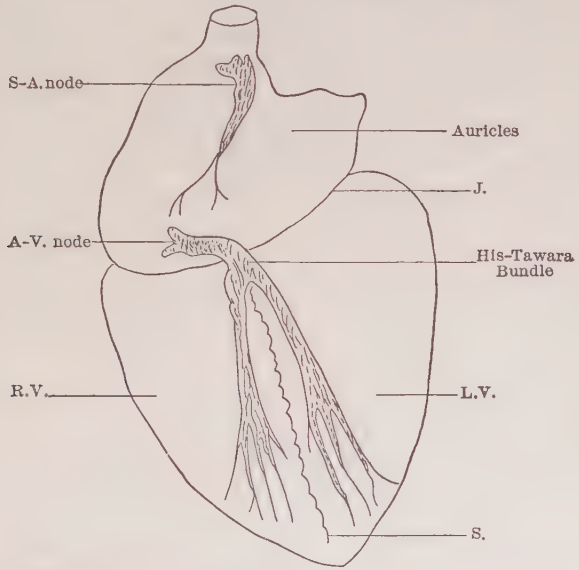


FIG. 111.—Diagram of heart showing relations of nodes to each other and to the His-Tawara Bundle (after Wiggers). *J.*, auriculo-ventricular junction; *S.*, ventricular septum; *L. V.*, left ventricle; *R. V.*, right ventricle.

auricle; it is designated the *sinoauricular* node, commonly abbreviated to S-A node; in the septum between the two auricles is a second similar cell-mass known as the *auricoloventricular* node (abbreviated to A-V node). The S-A node has muscle-like fibers ramifying from it to all parts of both auricles, and also to the A-V node; from the latter structure a special band of similar fibers (the His-Tawara Bundle) extends across the auriculoventricular junction (the latter being composed otherwise wholly of connective tissue) and terminates in intimate connection with the contracting fibers of the ventricular walls (Fig. 111).

The passage of the beat over the heart can be explained readily on two simple assumptions; first that the chemical processes going on in all fibers, nodal as well as contractile, are the same, consisting of an automatic breakdown of acid precursor, followed by the succeeding steps in contraction, and by the restorative reaction which serves to replenish the supply of acid-precursor; and second, that this restorative reaction is a very little quicker in the S-A node than elsewhere, next quicker in the A-V node, slightly slower yet in the auricular fibers, and much slowest of all in the fibers of the ventricles. Since, as stated above, the irritability of cardiac muscle increases steadily as acid-precursor accumulates, it is a fair assumption that the automatic breakdown occurs whenever a certain critical concentration of precursor is reached. It follows that the breakdown will ordinarily occur first in the S-A node, since the regeneration of precursor is quickest there; the effect will spread thence to the fibers of the auricles setting them into contraction, and by way of the A-V node to the ventricles, setting them off a brief instant later. Thus the S-A node is the *pacemaker* of the heart. Under ordinary circumstances none of the other regions ever get a chance to display their intrinsic automatic property, because always stimulated from the S-A node before their own has quite developed. A slight depression of the S-A node may, however, shift the function of pacemaker to the A-V node, with the result that instead of beating in sequence with the auricles the ventricles beat simultaneously with them.

Heart-Block. An injury to the specialized fibers that connect the nodes with the contractile fibers interferes with the normal spread of the beat over the heart. The effect, known as *heart-block*, is best seen when the injury is to the bundle that connects the A-V node to the ventricles. When that bundle is injured some or all the impulses from the A-V node fail to reach the ventricles. When some get across and some do not the ventricles "skip" beats whenever stimuli fail to reach them; if none of the impulses pass the point of injury the ventricles take on a spontaneous rhythm of their own, quite independent of, and much slower than the rhythm originating in the pacemakers. The first of these conditions is known as partial, the second as complete, heart-block.

Neurogenic and Myogenic Theories of the Heart-Beat. Before the significance of the pacemakers was thoroughly understood there was much discussion as to whether the automatic contractility of the heart depends on properties of its muscle-fibers (myogenic theory), or on stimuli originating in intrinsic nerves (neurogenic theory). We associate stimulation processes in the Body in general more commonly with nervous tissues than with any other kind, a fact which led many to maintain that the heart's action is probably neurogenic. The pacemakers, in which we now know the impulse to contraction to originate, are undoubtedly composed of modified muscle fibers, so that the myogenic origin of the beat can now be said to be established.

Events Occurring within the Heart during a Cardiac Cycle. The heart-beat obviously begins at the instant of discharge of the S-A node. Our account of the cardiac cycle will accordingly start at that point. The events to be placed in proper sequence are the flow of blood into and through the heart, and its ejection from the heart at systole; the contraction and relaxation of the chambers; the action of the heart-valves; and the heart-sounds. The time relations of the various events can best be indicated by a circular diagram (Fig. 112) since the events are all recurrent at regular intervals. The duration of the whole cycle is taken, for convenience, to be exactly 0.8 second (75 beats per minute). The diagram then divides into eight equal segments, each representing exactly 0.1 second. The outer of the two circular spaces is devoted to the auricles and the inner to the ventricles (both auricles act exactly together and so do both ventricles, hence only one space is needed for each kind of chamber); heavy shading indicates systole, light shading relaxation; absence of shading rest; the last two together make up diastole. The starting point of the diagram, *i. e.*, its uppermost point, is the instant of discharge of the S-A node. At this point, since both auricles and ventricles are inactive, blood is flowing from the veins directly through the first into the second, and since this has been going on for fully a half second ventricles as well as auricles have become pretty well filled. Almost instantly following discharge of the pacemaker the systole of the auricles begins, to continue for about a tenth of a second. The effect is to squeeze out the contained blood, and evidently in the direction that offers least resistance. The au-

riculoventricular (A-V) valves are open, and as there are no valves between the auricles and great veins, one channel would seem to be about as open as the other. But on the side toward the veins there is an inflowing stream of blood under slight, but definite pressure (see p. 389), while on the side toward the ventricle there is no obstacle except that presented by the soft and yielding ventricular walls, which distend readily as blood presses upon

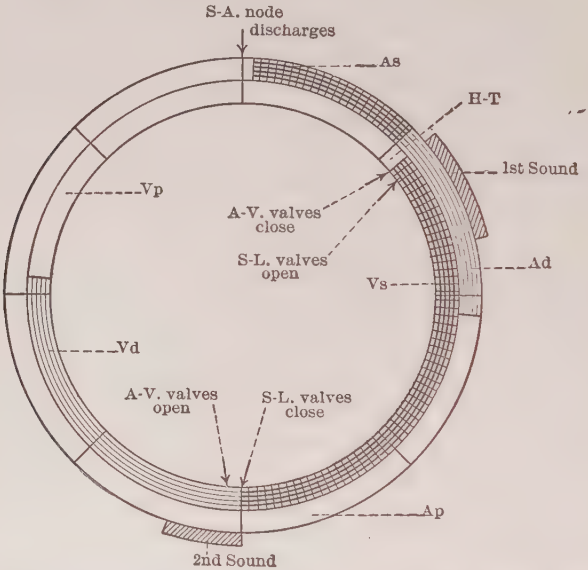


FIG. 112.—Diagram showing time relations of the cardiac cycle. Whole circle equals 0.8 second. *As*, auricular systole; *Ad* and *Ap* together, auricular diastole; *Vs*, ventricular systole; *Vd* and *Vp* together, ventricular diastole; *H-T*, passage of impulse over His-Tawara Bundle.

them. The result is that the auricles empty themselves into the ventricles, and while the pressure they exert stops the onward flow of venous blood for an instant there is no actual backward movement of it.

Following auricular systole there is a delay of a few hundredths of a second while the impulse passes from the A-V node over the His-Tawara Bundle to the ventricles; then ventricular systole begins, to continue about 0.3 second. This systole is a quick and forceful contraction of the ventricle walls, putting the blood within them under considerable pressure (for actual pressure

data see Fig. 113). The first effect of this pressure is to shut the auriculoventricular valves, so that no blood escapes backward into the auricles; the second is to open the semilunar (S-L) valves and eject the blood into the arteries, aorta in the case of the left heart, pulmonary artery in the case of the right. The effect of injecting this blood into the already distended arteries is to raise the pressure in them still further; accordingly at the instant ventricular systole ends, and relaxation begins, the semilunar valves snap shut. Continued relaxation removes all pressure of the ventricular walls on the contents of the ventricular cavities, and consequently the force which held the auriculoventricular valves shut while the ventricles were in contraction disappears; blood has been piling up meanwhile in the auricles, so that the auriculoventricular valves are promptly forced open. From this time until the beginning of the next cycle the entire heart is at rest and blood flows steadily from the veins through the auricles into the ventricles, nearly filling the latter by the time the pacemaker discharges again. As the ventricles fill, back currents are set up along their walls and these carry up the flaps of the auriculoventricular valves so that they are nearly closed when the systole of the auricles occurs.

Use of the Papillary Muscles. In order that the contracting ventricles may not force blood back into the auricles it is essential that the flaps of the mitral and tricuspid valves be maintained in position across the openings which they close, and be not pushed back into the auricles. At the commencement of the ventricular systole this is provided for by the cordæ tendineæ, which are of such a length as to keep the edges of the flaps in apposition, a position which is further secured by the fact that each set of cordæ tendineæ (Fig. 106) radiating from a point in the ventricle, is not attached around the edges of one flap but on the contiguous edges of two flaps, and so tends to pull them together. But as the contracting ventricles shorten, the cordæ tendineæ, if directly fixed to their interior, would be slackened and the valve-flaps pushed up into the auricle. The little papillary muscles prevent this. Shortening as the ventricular systole proceeds, they keep the cordæ taut and the valves closed.

Sounds of the Heart. If the ear be placed on the chest over the region of the heart during life, two distinguishable sounds

will be heard during each cardiac cycle. They are known respectively as the first and second sounds of the heart. The first is of lower pitch and lasts longer than the second and sharper sound: vocally their character may be tolerably imitated by the words *lubb, dŭp*. The first sound is heard during the early part of ventricular systole (Fig. 112). It is attributed in part to vibrations set up by the quickly and powerfully contracting muscles and in part to vibrations set up by the sudden closing of the auriculoventricular valves. In proof of this double origin is the observation that if the A-V valves are hooked back in a living animal the sound is altered but not abolished. The second sound is due to vibrations set up by the snapping shut of the semilunar valves and ceases if they be hooked back in a living animal.

In various forms of heart disease these sounds are modified or cloaked by additional "murmurs" which arise when the cardiac orifices are roughened or narrowed or dilated, or the valves inefficient. By paying attention to the character of the new sound then heard, the exact period in the cardiac cycle at which it occurs, and the region of the chest-wall at which it is heard most distinctly, the physician can often get important information as to its cause.

Action of the Heart Valves. The valves of the heart are entirely without rigidity. They consist of tough, but perfectly flaccid membranes, so that they respond perfectly to the forces which act upon them. This structure makes it inevitable that the valves will open whenever the pressure behind them is greater than that in front, and will close whenever the pressure in front is greater than that behind. During the whole diastole of the heart the pressure behind the auriculoventricular valves is greater than that in front of them; for in front is only the gradually filling cavity of the ventricle, while behind is the onward flow of blood from the great veins. During this time, therefore, these valves stand open. The systole of the auricle, by increasing the pressure behind, keeps them open until its end. During this same time the semilunar valves are shut, because in front of them are arteries whose walls are stretched with their load of blood and which, therefore, exert high pressure upon the valves, while behind are only the ventricular cavities, filling with blood. At the instant the ventricles begin to contract the situation with regard to the auriculoventricular valves changes. The relaxing auricles make room for the blood coming

in from the great veins and so release the pressure behind these valves; the contracting ventricle exerts pressure in front of them; they therefore close instantly. Since the semilunar valves remain closed until the rising pressure in the ventricle becomes greater than that in the aorta there is an instant at the beginning of ventricular systole when all the valves are shut. Again, at the beginning of ventricular diastole there is an instant when the ventricular pressure has fallen below that in the aorta but is still above the pressure in the auricles; during this time, again, the valves of the heart are all shut.

In Fig. 113 the pressure changes in left auricle, left ventricle, and aorta throughout the cardiac cycle are represented graphically.

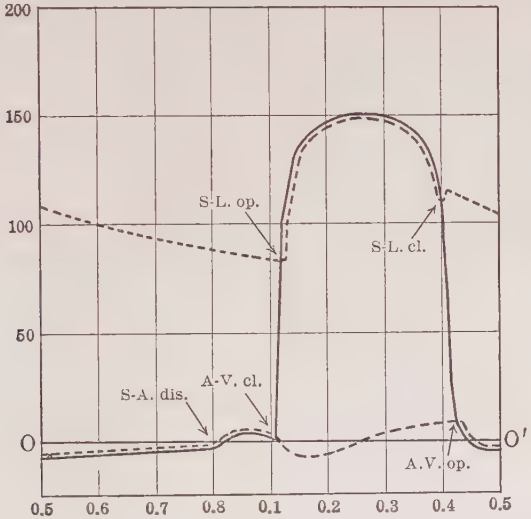


FIG. 113.—Pressure changes in auricle, ventricle, and aorta during cycle of left heart. *O-O'*, atmospheric base line; figures on left vertical line represent pressures in mm. Hg.; figures at bottom represent time intervals in tenths of a second. The cycle is presumed to begin and end at 0.8, *i. e.*, at the instant of discharge of the *S-A* node. The solid line shows pressure changes in the ventricle, the lower dotted line in the auricle, and the upper dotted line in the aorta. The action of the valves is indicated on the diagram: *op* = open; *cl* = close; *A-V* = auriculo-ventricular; *S-L* = semilunar.

In studying the curves one should bear in mind that whenever auricular pressure is above ventricular the A-V valves must necessarily be open and vice versa, and whenever ventricular pressure is above aortic the S-L valves must be open and vice versa; further-

more that a rise of pressure means either active contraction of the region in which the rise occurs, or the forcing of blood under pressure from a region of active contraction to the one in which the rise is observed. If these points are kept in mind the facts indicated in Fig. 113 can be correlated with those shown in Fig. 112 and with the general account given above, to form a clear picture of the cardiac cycle as a whole. The figures given are for the left heart; the right heart is less powerful, so that the maximum pressures in ventricle and pulmonary artery are considerably lower than those cited for the left heart; in other respects the curves would answer about as well for one as for the other.

Effects of Valvular Insufficiency. The commonest heart troubles are due to failure of one or other of the valves to close perfectly. The mechanical effect of such inefficiency is, of course, a back rush of blood through the leaky valve. The effects on the Body at large will depend on which valve is inefficient. Leakage of the semilunars means a return into the ventricle of part of the blood just pumped out. The circulation is to that extent less effectively maintained. The heart usually compensates for this defect by muscular growth (hypertrophy) by which it becomes enough more powerful than normal to make up for the lessened efficiency. Leakage of an auriculoventricular valve is much more serious because it permits a jet of blood to be driven backward into the veins at each heart-beat under the driving force of the powerful ventricular contraction. The small veins and capillaries are not adapted to receive such a hammering and are injured thereby. If the leaky valve is the mitral the lung capillaries are the ones affected. If the tricuspid is inefficient the backward surge makes itself felt in distant organs. Kidney impairment is a common sequel to this type of valvular disease. Inflammatory rheumatism frequently brings on valve trouble. In fact the danger of this outcome is so great that every pains should be taken to avoid it, by giving the patient the best of care and treatment.

Function of the Auricles. The ventricles have to do the work of pumping the blood-through the blood vessels. Accordingly their walls are far thicker and more muscular than those of the auricles; and the left ventricle, which has to force the blood over the Body generally, is stouter than the right, which has only to send blood around the comparatively short pulmonary circuit. The circu-

lation of the blood is in fact maintained by the ventricles, and we have to inquire what is the use of the auricles. Not unfrequently the heart's action is described as if the auricles first filled with blood and then contracted and filled the ventricles; and then the latter contracted and drove the blood into the arteries. From the account given above, however, it will be seen that the events are not accurately so represented, but that during all the pause blood flows on through the auricles into the ventricles, which latter are already nearly full when the auricles contract; this contraction merely completing their filling. The real use of the auricles is to afford a reservoir into which the veins may empty while the comparatively long-lasting ventricular contraction is taking place.

If the heart consisted of the ventricles only, with valves at the points of entry and exit of the blood, the circulation could be maintained. During disatole the ventricle would fill from the veins, and during systole empty into the arteries. But in order to accomplish this, during the systole the valves at the point of entry must be closed, or the ventricle would empty itself into the veins as well as into the arteries; and this closure would necessitate a great loss of time which might be utilized for feeding the pump. This is avoided by the auricles, which are really reservoirs at the end of the venous system, collecting blood when the ventricular pump is at work. When the ventricles relax, the blood entering the auricles flows on into them; but previously, during the part of the cardiac cycle occupied by the ventricular systole, the auricles have accumulated blood, and when they at last contract they send on into the ventricles this accumulation.

Ventricular Output, and Blood-Flow per Minute. A quantity very advantageous to know is the amount of blood discharged from the heat at each beat. The number of beats per minute can be determined with ease by simply counting the pulse; multiplying this by the quantity per beat gives the total volume of blood passing around the circulation per minute. Since the tissues are immediately dependent on the blood supply for the materials they use in metabolism and as a receptacle for wastes (p. 309), there is a close relationship between the amount of blood flowing through the tissue capillaries per unit of time and the metabolic activities that the tissues are maintaining. This general relationship has long been known; in fact one of the most familiar of bodily adjust-

ments is the increase in pulse rate that attends any increase in functional metabolism (muscular exercise for example). Until recently it has not been known certainly whether the heart pumps always the same amount per beat, or sometimes more and sometimes less. It is obviously impossible to measure the output of the heart directly; methods have lately been devised, however, by which the blood-flow through the lungs can be determined accurately. But all the blood from the right heart has to pass through the lungs; furthermore, the output of the right heart must be exactly equal minute by minute, if not beat by beat, to that of the left heart to avoid piling up of blood in some part of the circulation; it follows that if the blood-flow through the lungs can be determined that through the heart can be calculated. The various methods need not be described here in detail. A very good one depends on inhaling known amounts of some harmless vapor which is taken up by the blood from the air in the lungs, and determining how much of the vapor is taken up by subtracting the quantity exhaled from that inhaled; knowing how much of the vapor each cubic centimeter of blood can hold, a simple calculation shows how much blood must have passed through the lungs during the experiment.

The results of such experiments show that in a man weighing 70 kilograms (154 lbs.) at rest each ventricle discharges about 100–110 cubic centimeters per beat. In vigorous muscular exercise the amount more than doubles, rising to about 240 c. c. There is also at such times an increase in heart-rate from an average of about 70 to 150 or so. The total blood-flow per minute may thus increase from a resting value of something like 7,400 c. c. per minute (70×105) to around 36,000 c. c. (150×240) in vigorous exercise.

The Work Done by the Heart. According to the physical definition work is measured by the weight lifted times the height to which it is raised. In estimating the work of the heart we substitute for the height the resistance against which the heart works. In the Body at rest this resistance is equivalent in the left ventricle to that of a column of blood about two meters high, and for the right ventricle about 0.8 meter. The mass of blood ejected from each ventricle is, as shown above, about 110 grams. The work calculated from these data would give for the left heart $110 \times 2 = 220$ grammeters, and for the right heart $110 \times 0.8 = 88$ grammeters.

Since the heart in addition to moving the weight of blood imparts to it a considerable velocity, it is necessary to add to the amounts of work calculated above an additional amount to represent that required to impart to the blood its velocity. This latter amount approximates 3 grammeters. The total work output of the heart per beat in the resting Body is, therefore, roughly 311 grammeters, equivalent in the English scale to about 2 foot-pounds. When the heart is beating at the rate of 70 per minute it does 140 foot-pounds per minute, making it a 240th horse-power engine. If it maintained this rate throughout the entire twenty-four hours of the day it would do in that time 200,000 foot-pounds of work, an amount equivalent to that done by the leg muscles of a man weighing 150 pounds in climbing a mountain 1,300 feet high.

During active exercise the discharge per beat more than doubles; the resistance to be overcome increases about 50 per cent; and there is also a decided increase in velocity. The combined effect is to multiply the work per beat by about three. Since the pulse rate may double at the same time, the work per minute may increase sixfold; in other words, the heart may become for the time being a 40th horse-power engine. This is approximately a maximum figure, attainable only in fairly short spurts. In sustained exercise it is probable that the circulation becomes adjusted so that the heart works not more than two or three times as hard as when the Body is at rest.

That the heart is able to do such amounts of work daily without fatigue, and keep it up day in and day out for seventy or more years, is due to its ability to recover quickly from the effects of its activity, coupled with the fact that in a whole day its resting time considerably outweighs the time during which it is active. The heart-beat is ordinarily much slower during sleep than during waking; as the result the heart enjoys an "eight-hour day" if only its actual contraction time be counted.

The Extrinsic Nerves of the Heart. The heart, as stated previously, is under the control of the autonomic system. It receives nerve-fibers both from the cranial and thoracico-lumbar systems. The cranial autonomic fibers reach it by way of the tenth cranial nerves, the vagi, the thoracico-lumbar by way of sympathetic ganglia. The vagus nerves give off their cardiac branches in the

neck; the cardiac nerves from the thoracico-lumbar system arise from the inferior cervical ganglion, a sympathetic ganglion lying in the lower neck region. Both anatomically and physiologically the two sets of nerve-fibers are distinct. Anatomically the vagus fibers are pre-ganglionic; they arise from cell-bodies in the nucleus of the tenth nerve in the medulla and are myelinated. They terminate about nerve-cells lying on or within the heart itself. The fibers from the sympathetic system are post-ganglionic; they arise from cell-bodies in sympathetic ganglia, the inferior cervical for the most part, and are non-myelinated. They terminate in the tissues of the heart directly. Since nicotine cuts the connection between pre- and post-ganglionic fibers, application of that drug to the nerve cells of the heart abolishes the influence of the vagi, but does not affect the thoracico-lumbar control at all.

Physiologically the vagus fibers are *inhibitory;* their stimulation slows and weakens the heart-beat. When very strongly stimulated they may bring the heart to a complete standstill, although in mammals the standstill is maintained for a few seconds only, the heart soon "breaking through" the inhibition. The thoracico-lumbar fibers have precisely the opposite function, being *augmentor;* their stimulation accelerates and strengthens the beat of the heart.

In addition to the efferent autonomic innervation just described the heart is provided with a set of afferent nerve-fibers. These reach the central nervous system either by way of the vagus nerves, or in some species of animals, rabbits for example, as separate nerve-trunks known as the *depressor* nerves. The function of these afferent fibers will be discussed in Chap. XXII in connection with the nervous control of the blood vessels.

The Inhibitory and Augmentor Centers. The control of the heart-beat is reflex in its nature, and like most other "vital" processes which are subject to reflex control is vested in certain "centers" of the medulla. Two heart-regulating centers are recognized, the *cardio-inhibitory* center and the *cardio-augmentor* center. The inhibitory center is in the nuclei of the tenth nerve. It is bilateral, each side containing half of it. The exact position of the augmentor center has not been determined. It is probably not a compact mass of cells as is the inhibitory center, but is scattered diffusely through the medulla.

Both these centers are in the path of all incoming impulses, and there is evidence that both of them are kept in constant "tonic" activity through the incessant play of stimuli upon them. Of recent years the view has been gaining ground that the tonic activity of the "vital" centers is maintained, in part at least, by chemical influences exerted through the blood. This influence has long been known to exist in the case of the respiratory center. That it is a factor in the regulation of the heart seems also to be now well established.

The heart is thus constantly receiving both inhibitory and augmentor impulses, the former tending to diminish its activity, the latter to increase it. The actual heart-beat is the expression, therefore, of the balance between two opposing tendencies, and its increase or decrease indicates that one or the other has gained the advantage.

In attempting to analyze the causes of changes in the heart-rate it must be remembered that an increase in rate may mean either an increase in the activity of the augmentor center, or a depression of the inhibitory center. Conversely, a decrease in rate may mean either a depression of the augmentor center or an increase in the activity of the inhibitory center. An observation that helps us in deciding which of the centers may have been responsible for any observed change is that the inhibitory mechanism acts much more promptly than does the augmentor. Any change that follows quickly an exciting cause is, therefore, to be attributed to the inhibitory mechanism. Since the heart, as a matter of fact, responds almost instantly to most influences we are in the habit of looking upon the augmentor mechanism as affording a fairly steady background of augmentor excitation upon which the inhibitory mechanism may play in delicate adjustment to the needs of the circulation. There is a perceptible quickening of the beat with any muscular movement, at least with any as extensive as that required to press a telegraph key. The quickening shows itself in the next beat after the beginning of the movement. The suggestion has been made that during the discharge of the exciting nervous impulses from the brain to the muscles, there is *irradiation* in the brain stem unto the inhibitory center; that this irradiation depresses the center, and so allows a quickening of the beat.

There are certain conditions in which the augmentor center seems to show heightened activity. After muscular exercise there is a more or less persistent acceleration of the heart that appears to be due to stimulation of the augmentor center by the waste products of muscular activity which persist for a time in the circulating blood. The maximal acceleration of the heart seen in vigorous exercise is undoubtedly the combined result of both influences: depression of the inhibitory and stimulation of the augmentor center. The acceleration of the heart in time of emotional stress or of great pain is to be explained, as stated previously, through the connection of the augmentor mechanism with the thoracico-lumbar autonomic, the emergency, system.

The familiar changes of heart-rate with changes of posture, slowed when lying, quickened with sitting or standing, are apparently the results of the redistribution of the blood over the Body under the influence of gravity. The quickening of the beat when one stands erect is undoubtedly an adaptation designed to overcome the tendency of the blood to accumulate in the lower parts of the Body when in this position; but how the adaptation is brought about is not known. Successive swallowing, as in sipping water, increases the heart-rate by depressing the inhibitory center. A blow over the stomach (the solar plexus) gives rise to afferent impulses which stimulate the inhibitory center; the heart-rate is therefore diminished.

These are all illustrations of the general rule that the heart-beat may be modified by sensory stimulations. It is a matter of ordinary observation that many experiences, particularly those involving sensory impressions of high intensity, are accompanied by marked changes in heart-rate.

In connection with this analysis of the control of the heart-beat the importance of obtaining the proper viewpoint for considering physiological processes may well be emphasized. If one who has not studied the subject particularly be asked why running makes the heart beat faster he will probably answer that exercising muscles require more blood than resting ones, and that the heart beats faster to furnish this extra amount. A moment's thought shows that this statement, though quite true, does not really answer the question. It implies that the heart has knowledge of the needs of the tissues, which, of course, it cannot have.

The increased heart-rate which accompanies exercise is undoubtedly an adaptive response, as are most reflex responses, but its explanation resides, not in the adaptation, but in the reflex mechanism which brings it about. We should be continually on guard against the tendency to explain physiological processes by their results rather than by the means by which the results are accomplished.

CHAPTER XXI

THE CIRCULATION OF THE BLOOD. BLOOD-PRESSURE AND BLOOD-VELOCITY. THE PULSE

The Flow of the Blood Outside of the Heart. The blood leaves the heart intermittently and not in a regular stream, a quantity being forced out at each systole of the ventricles: before it reaches the capillaries, however, this rhythmic movement is transformed into a steady flow, as may readily be seen by examining under the microscope thin transparent parts of various animals, as the web of a frog's foot, a mouse's ear, or the tail of a small fish. In consequence of the steadiness with which the capillaries supply the veins the flow in these is also unaffected, directly, by each beat of the heart; if a vein be cut the blood wells out uniformly, while from a cut artery the blood spurts out not only with much greater force, but in jets which are much more powerful at regular intervals corresponding with the systoles of the ventricles.

The Circulation of the Blood as Seen in the Frog's Web. There are few more fascinating or instructive phenomena than the circulation of the blood as seen with the microscope in the thin membrane between the toes of a frog's hind limb. Upon focusing beneath the epidermis a network of minute arteries, veins, and capillaries, with the blood flowing through them, comes into view (Fig. 114). The arteries, *a*, are readily recognized by the fact that the flow in them is fastest and from larger to smaller branches. The latter are seen ending in capillaries, which form networks, the channels of which are all nearly equal in size. While in the veins arising from the capillaries the flow is from smaller to larger trunks, and slower than in the arteries, but faster than in the capillaries.

The reason of the slower flow of the capillaries is that their united area is considerably greater than that of the arteries supplying them, so that the same quantity of blood flowing through them in a given time has a wider channel to flow in and moves slowly. The area of the veins is smaller than that of the capillaries

but greater than that of the arteries, and hence the rate of movement in them is also intermediate. Always when an artery divides, the area of its branches is greater than that of the main trunk, and so the arterial current becomes slower and slower from the heart onwards. In the veins, on the other hand, the area of a trunk formed by the union of two or more branches is less than that

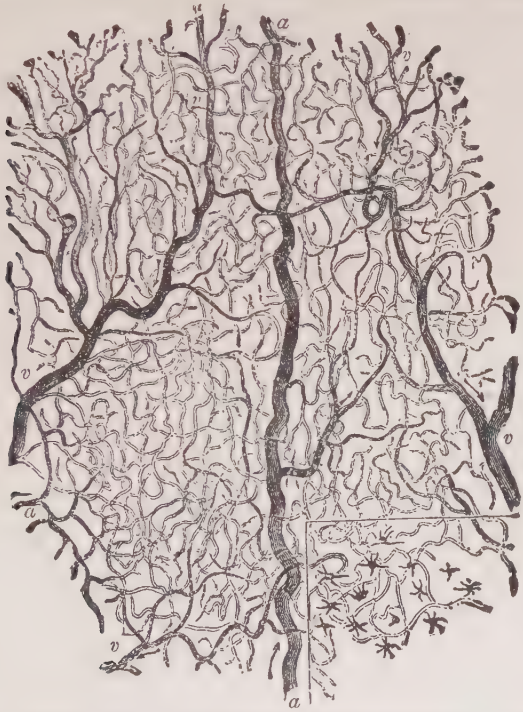


FIG. 114.—A small portion of the capillary network as seen in the frog's web when magnified about 25 diameters. *a*, a small artery feeding the capillaries; *v*, *v*, small veins carrying blood back from the latter.

of the branches together, and the flow becomes quicker and quicker towards the heart. But even at the heart the united cross-sections of the veins entering the auricles are greater than those of the arteries leaving the ventricles, so that, since as much blood returns to the heart in a given time as leaves it, the rate of the current in the pulmonary veins and the venæ cavæ is less than in the pulmonary artery and aorta. We may represent the vascular system as a double cone, widening from the ventricles to the capillaries

and narrowing from the latter to the auricles. Just as water forced in a narrow end of this would flow quickest there and slowest at the widest part, so the blood flows quickest in the aorta and slowest in the capillaries, which taken together form a much wider channel.

The Axial Current and the Inert Layer. If a small artery in the frog's web be closely examined it will be seen that the rate of flow is not the same in all parts of it. In the center is a very rapid current carrying along all the red corpuscles and known as the *axial stream*, while near the wall of the vessel the flow is much slower, as indicated by the rate at which the pale blood-corpuscles are carried along in it. This is a purely physical phenomenon. If any liquid be forcibly driven through a fine tube which it wets, water for instance through a glass tube, the outermost layers of the liquid will remain nearly motionless in contact with the tube; the next layers of molecules will move a little, the next faster still; and so on until a rapid current is found in the center. If solid bodies, as powdered sealing-wax, be suspended in the water, these will all be carried on in the central faster current or *axial stream*, just as the red corpuscles are in the artery. The white corpuscles, partly because of their less specific gravity, and partly because of their sometimes irregular form, due to amœboid movements, get frequently pushed out of the axial current, so that many of them are found in the inert layer.

The Resistance to the Blood-Flow. As liquid flows through a tube there is a certain amount of friction between the moving liquid and the walls of the tube. There is also friction between the different concentric layers of the liquid, since each of them is moving at a different rate from that in contact with it on each side. This form of friction is known in hydrodynamics as "internal friction," and it is of great importance in the circulation of the blood. The friction increases very fast as the caliber of the tube through which the liquid flows diminishes: so that with the same rate of flow it is disproportionately much greater in a small tube than in a larger one. Hence a given quantity of liquid forced in a minute through one large tube would experience much less resistance from friction than if sent in the same time through four or five smaller tubes, the united transverse sections of which were together equal to that of the single larger one. In the blood vessels the increased total area, and consequently slower flow, in

the smaller channels partly counteracts this increase of friction, but only to a comparatively slight extent; so that the friction, and consequently the resistance to the blood-flow, is far greater in the capillaries and arterioles than in the small arteries, and in the small arteries than in the large ones. Practically we may regard the arteries as tubes ending in a sponge: the united areas of all the channels in the latter might be considerably larger than that of the supplying tubes, but the friction to be overcome in the flow through them would be much greater.

The Conversion of the Intermittent into a Continuous Flow. Since the heart sends blood into the aorta intermittently, we have still to inquire how it is that the flow in the capillaries is continuous. In the larger arteries it is not, since we can feel them dilating as the "*pulse*," on applying the finger over the radial artery at the wrist, or over the temporal artery on the side of the brow.

The first explanation which suggests itself is that since the capacity of the blood vessels increases from the heart to the capillaries, an acceleration of the flow during the ventricular contraction which might be very manifest in the vessels near the heart would become less and less obvious in the more distant vessels. But if this were so, then when the blood was collected again from the wide capillary sponge into the great veins near the heart, which together are but little bigger than the aorta, we ought to find a pulse, but we do not: the venous pulse which sometimes occurs having quite a different cause, being due to a back-flow from the auricles, or a checking of the on-flow into them, during the cardiac systole. The rhythm of the flow caused by the heart is therefore not merely cloaked in the small arteries and capillaries, but abolished in them.

We can, however, readily contrive conditions outside the Body under which an intermittent supply is transformed into a continuous flow. Suppose we have two vessels, *A* and *B* (Fig. 115) containing water and connected below in two ways: through the tube *a* on which there is a pump *c* provided with valves so that it can only drive liquid from *A* to *B;* and through *b*, which may be left wide open or narrowed by the clamp *e*, at will. If the apparatus be left at rest the water will lie at the same level, *d*, in each vessel. If now we work the pump, at each stroke a certain amount of

water will be conveyed from A to B, and as result of the lowering of the level of liquid in A and its rise in B, there will be immediately a return flow from B to A through the tube b. A, in these circumstances, would represent the venous system, from which the heart constantly pumps blood into B, representing the arterial system; and b would represent the capillary vessels through which the return flow takes place; but, so far, we should have as intermittent a flow through the capillaries, b, as through the heart-pump, a. Now imagine b to be narrowed at one point so as to oppose resistance to the back-flow, while the pump goes on working steadily. The result will be an accumulation of water in B, and a fall of its level in A. But the more the difference of level in the two vessels increases, the greater is the force tending to drive water back through b to A, and more will flow back, under the greater difference of pressure, in a given time, until at last, when the water in B has reached a certain level, d', and that in A has correspondingly fallen to d'', the current through b will carry back in one minute just so much water as the pump sends the other way, and this back-flow will be nearly constant; it will not depend directly upon the strokes of the pump, but upon the head of water accumulated in B; which head of water will, it is true, be slightly increased at each stroke of the pump, but the increase will be very small compared with the whole driving force, and its influence will be inappreciable. We thus gain the idea that an incomplete impediment to the flow from the arteries to the veins (from B to A in the diagram), such as is afforded by friction in the capillaries, may bring about conditions which will lead to a steady flow along the latter vessels.

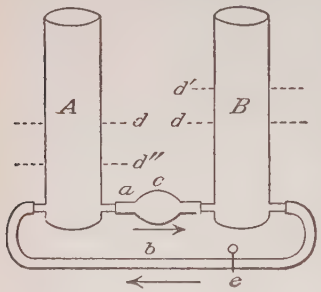


Fig. 115.

But in the arterial system there can be no accumulation of blood at a higher level than that in the veins, such as is supposed in the above apparatus; and we must next consider if the "head of water" can be replaced by some other form of driving force. It is in fact replaced by the elasticity of the large arteries. Suppose an elastic tube (B, Fig. 116) instead of the vessel B connected

with the pump *c*. If there be no resistance to the back-flow the current through *b* will be discontinuous. But if resistance be interposed, as by clamping off *b*, and so forcing the liquid through the capilliary tubes indicated by *b'* (Fig. 116), then the elastic tube will become distended, since the pump sends in a given time more liquid into it than it passes back through *b'*. But the more it becomes distended the more will it squeeze the liquid inside and the faster will it send that back to *A*, until at last its squeeze is so powerful that each minute or two or five minutes it sends back into *A* as much as it receives. Thenceforth the back-flow through *b'* will be practically constant, being immediately dependent upon

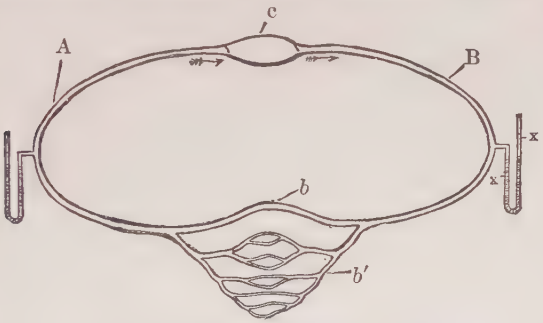


FIG. 116.—Diagram of Weber's Schema.

the elastic reaction of the tube, and only indirectly upon the action of the pump which keeps it distended. Such a state of things represents very closely the phenomena occurring in the blood vessels. The highly elastic large arteries are kept stretched with blood by the heart; and the reaction of their elastic walls, steadily squeezing on the blood in them, forces it continuously through the small arteries and capillaries. The steady flow in the latter depends thus on two factors: first, the elasticity of the large arteries; and secondly, the resistance to their emptying, dependent upon internal friction in the small arteries and the capillaries, which calls into play the elasticity of the large vessels. Were the capillary resistance or the arterial elasticity absent the blood-flow in the capillaries would be rhythmic.

Arterial Pressure. The condition of things just described represents very closely the phenomena presented in the blood-vascular system, in which the ventricles of the heart, with their

auriculoventricular and semilunar valves, represent the pump *c*, the smallest arteries and the capillaries the resistance at *b'*, the large arteries the elastic tube *B*, and the veins the tube *A*. The ventricles constantly receiving blood through the auricles from the veins, send it into the arteries, which empty themselves with difficulty through the capillaries, and so blood accumulates in them until the elastic reaction of the stretched arteries is able to squeeze in a minute through the capillaries just so much blood as the left ventricle pumps into the aorta, and the right into the pulmonary artery, in the same time. Accordingly in a living animal a pressure-gauge connected with an artery (*x*, Fig. 116) shows a much higher pressure than one connected with a vein, and this persisting difference of pressure, only increased by a small fraction of the whole at each heart-beat, brings about a steady flow from the arteries to the veins. The heart keeps the arteries stretched and the stretched arteries maintain the flow through the capillaries, and the constancy of the current in them depends on two factors: (1) the resistance experienced by the blood in its flow from the ventricles to the veins, and (2) the elasticity of the larger arteries which allows the blood to accumulate in them under a high pressure, in consequence of this resistance.

Since the blood flows from the aorta to its branches and from these to the capillaries and thence to the veins, and liquids in a set of continuous tubes flow from points of greater to those of less pressure, it is clear that the blood-pressure must constantly diminish from the aorta to the right auricle; and similarly from the pulmonary artery to the left auricle. At any point, in fact, the pressure is proportionate to the resistance in front, and since the farther the blood has gone the less of this, due to impediments at branchings and to internal friction, it has to overcome in finishing its round, the pressure on the blood diminishes as we follow it from the aorta to the venæ cavæ. In the larger arteries the fall of pressure is gradual and small, since the amount of resistance met with in the flow through them is but little. In the small arteries and capillaries the resistance overcome and left behind is (on account of the great internal friction due to their small caliber) very great, and consequently the fall of pressure between the medium-sized arteries and the veins is rapid and considerable.

Modifications of Arterial Pressure by Changes in the Heart-Beat. A little consideration will make it clear that the pressure prevailing at any time in a given artery depends on two things—the rate at which the vessel is filled, *i. e.*, upon the amount of work done by the heart; and the ease or difficulty with which it is emptied, that is, upon the resistance in front. A third factor has to be taken into account in some cases; namely, that when the muscular coats of the small arteries contract the local capacity of the vascular system is diminished, and has to be compensated for by greater distention elsewhere, and *vice versa*. This would of itself of course bring about changes in the pressure exerted on the contained liquid, but for the present it may be left out of consideration. If we suppose a system such as represented in Fig. 116, to be in equilibrium, with the pump injecting into B a certain volume of liquid per minute, and the elastic tension of the tube B just sufficient to force that volume through the resistance b' in the same time, it is clear that the mean pressure indicated on the gauge x will be very nearly constant. If, now, the volume of liquid forced into B in a minute be increased, either by the pump working faster or by its pumping more at each stroke, there will evidently be an accumulation in B, since its tension is adjusted to force out the less volume per minute, but this accumulation, by stretching the tube still more, increases its elastic tension, so that this is presently great enough to force out the added volume as fast as it comes in. The pressure-gauge will now stand at a higher point, showing that the contents of the tube are under greater pressure than before. Similarly, a diminution in the influx of liquid into B will be followed by a fall of pressure within it as the walls of the tube adjust themselves to the smaller volume to be forced out per minute. Precisely the same reasoning may be applied to the vascular system for determining the effects upon arterial pressure of changes in the heart-beat.

Modifications of Arterial Pressure by Changes in the Peripheral Resistance. If while the pump c in Fig. 116 is steadily sending a given volume of liquid per minute into B the resistance at b' increase, it is clear arterial pressure must rise. For B is only stretched enough to squeeze out in a minute the given quantity of liquid against the original resistance, and cannot at first send out that quantity against the greater. Liquid will consequently

accumulate in it until at last it becomes stretched enough to send out as much in a minute as before in spite of the greater resistance to be overcome. A new mean pressure at a higher level will then be established. If, on the contrary, the resistance diminishes while the pump's work remains the same, then *B* will at first squeeze out in a minute more than it receives, until finally its elastic pressure is reduced to the point at which its receipts and losses balance, and a new and lower mean pressure will be established in *B*.

Similarly in the vascular system, increase of the peripheral resistance by narrowing of the small arteries will increase arterial pressure in all parts nearer the heart, while dilation of the small arteries will have the contrary effect.

Summary. We find then that arterial pressure at any moment is dependent upon: (1) the quantity of blood forced into the arteries in a given time; (2) the caliber of the smaller vessels. Both of these and consequently the capillary circulation which depends upon arterial pressure, are under the control of the nervous system (see Chaps. XX and XXII).

The Pulse. When the left ventricle contracts it forces a certain amount of blood into the aorta, which is already distended, and on account of the resistance in front cannot empty itself as fast as the contracting ventricle fills it. As a consequence its elastic walls yield still more—it enlarges both transversely and longitudinally and if exposed in a living animal can be seen and felt to pulsate, swelling out at each systole of the heart, and shrinking and getting rid of the excess during the pause. A similar phenomenon can be observed in all the other large arteries, for just as the contracting ventricle fills the aorta faster than the latter empties (the whole period of diastole and systole being required by the aorta to pass on the blood sent in during systole), so the increased tension in the aorta immediately after the cardiac contraction drives on some of its contents into its branches, and fills these faster than they are emptying, and so causes a dilatation of them also, which only gradually disappears as the aortic tension falls before the next systole. Hence after each beat of the heart there is a sensible dilation of all the larger arteries, known as the *pulse*, which becomes less and less marked at points on the smaller branches farther from the heart, but which in health can readily

be recognized on any artery large enough to be felt by the finger through the skin. The radial artery near the wrist, for example, will always be felt tense by the finger, since it is kept overfilled by the heart in the way already described. But after each heart-beat it becomes more rigid and dilates a little, the increased distension and rigidity gradually disappearing as the artery passes on the excess of blood before the next heart-beat. The pulse is then a wave of increased pressure started by the ventricular systole, radiating from the semilunar valves over the arterial system, and gradually disappearing in the smaller branches. In the aorta the pulse is most marked, for the resistance there to the transmission onwards of the blood sent in by the heart is greatest, and the elastic tube in which it consequently accumulates is shortest and so the increase of pressure and the dilation caused are considerable. The aorta, however, gradually squeezes out the excess blood into its branches, and so this becomes distributed over a wider area, and these branches having less resistance in front find less and less difficulty in passing it on; consequently the pulse-wave becomes less and less conspicuous and finally altogether disappears before the capillaries are reached, the excess of liquid in the whole arterial system after a ventricular systole being too small to raise the mean pressure sensibly once it has been widely distributed over the elastic vessels, which is the case by the time the wave has reached the small branches which supply the capillaries.

The pulse-wave travels over the arterial system at the rate of about 7 meters (22.4 feet) in a second. The blood itself does not of course travel as fast as the pulse-wave, for that quantity sent into the aorta at each heart-beat does not immediately rush on over the whole arterial system, but by raising the local pressure causes the vessel to squeeze out faster than before some of the blood it already contains, and this entering its branches raises the pressure in them and causes them more quickly to fill their branches and raise the pressure in them; the pulse-wave or wave of increased pressure is transmitted in this way much faster than any given portion of the blood. How the wave of increased pressure and the liquid travel at different rates may be made clearer perhaps by picturing what would happen if liquid were pumped into one end of an already full elastic tube, closed at the other end.

At the closed end of the tube a dilation and increased tension would be felt immediately after each stroke of the pump, although the liquid pumped in at the other end would have remained about its point of entry; it would cause the pulsation not by flowing along the tube itself, but by giving a push to the liquid already in it. If instead of absolutely closing the distal end of the tube one brought about a state of things more nearly resembling that found in the arteries by allowing it to empty itself against a resistance, say through a narrow opening, the phenomena observed would not be essentially altered; the increase of pressure would travel along the distended tube far faster than the liquid itself.

The pulse being dependent on the heart's systole, "feeling the pulse" of course primarily gives a convenient means of counting the rate of beat of that organ. To the skilled touch, however, it may tell a great deal more, as for example whether it is a readily compressible or "soft pulse" showing a low arterial pressure, or tense and rigid ("a hard pulse") indicative of high arterial pressure, and so on. In adults the normal pulse-rate may vary from sixty-five to seventy-five, the most common number being seventy-two. In the same individual it is faster when standing than when sitting, and when sitting than when lying down. Any exercise increases its rate temporarily, and so does excitement; a sick person's pulse should not therefore be felt when he is nervous or excited (as the physician knows when he tries first to get his patient calm and confident), as it is then difficult to draw correct conclusions from it. In children the pulse is quicker than in adults, and in old age slower than in middle life.

The Measurement of Blood-Pressure. Direct determinations of arterial and venous pressures are made in living, anesthetized animals by inserting into a large artery or vein a glass tube connected with a pressure-gauge. The usual form of gauge for such work is the *mercury manometer* represented in Fig. 117. This instrument, on account of the great inertia of mercury, follows only slightly the rapid fluctuations of pressure due to the beats of the heart. It therefore gives mean or average pressures. Results obtained with mercury manometers are expressed in terms of the height of the mercury column sustained by the blood-pressure. To reduce them to columns of blood they

must be multiplied by 13.6, the number of times mercury is heavier than blood. The mean aortic pressure in average-sized dogs is ordinarily not far from 140 millimeters of mercury. The pressure in the veins diminishes from 3 or 4 millimeters of mercury in the

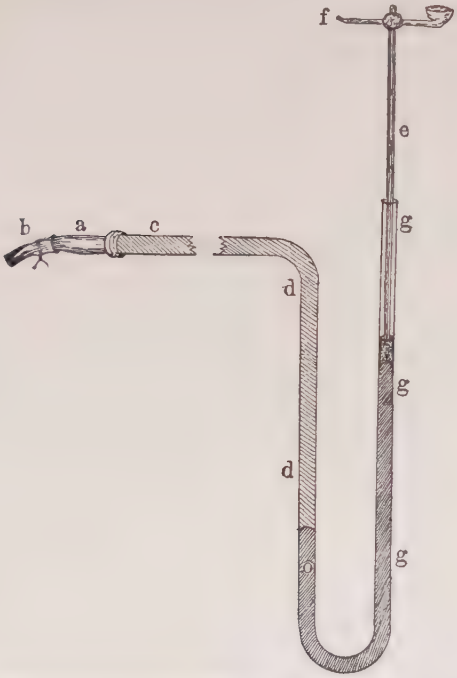


FIG. 117.—Mercury manometer for recording blood-pressure. *d g*, glass U-tube partly filled with mercury. In one limb is borne a float, *e*, bearing a recording device *f*; the other limb is filled with a suitable liquid and connected water-tight with the heart end of a divided artery *b*, by means of glass connection *a*. Changes in the mercury level indicate changes of arterial pressure.

large veins of the front leg to zero at the entrance to the auricle (see p. 365).

Blood-Pressure in Man. In man it is necessary to determine blood-pressures by methods that do not involve operative procedure. Various devices are in use for this purpose. They depend on the fact that bodily tissues, being for the most part liquid, are virtually incompressible and so transmit throughout their extent pressures applied to them. For determining arterial pressures the upper arm is inclosed in a cuff of hollow rubber

tubing so arranged that its inflation presses from all sides on the arm. The cuff is inflated until its pressure on the arm is just sufficient to squeeze shut the brachial artery. By means of a manometer attached to the cuff the amount of pressure applied can be determined. The differences between the various forms of instruments depend chiefly on their methods for determining exactly when the artery is occluded. These instruments do not give mean blood-pressures, as does the mercury manometer, but maximum (systolic) and minimum (diastolic) pressures. It is found that in man the systolic pressure averages from 110 to 120 mms. of mercury, and the diastolic about 80 mms. of mercury.

Determinations of capillary and venous pressures in man can be made more easily than determinations of arterial pressure because there are superficial capillaries and veins whose occlusion can be observed directly; in capillaries by whitening of the skin, in veins by the disappearance of the vein-ridge along it. The basis of the method is the same as for arterial pressure, namely, determination of the pressure necessary to occlude the vessel. Capillary pressures measured by this method average about 22 mms. of mercury; venous pressures 10 mms. or less.

The Rate of the Blood-Flow. As the vascular system becomes more capacious from the aorta to the capillaries the rate of flow in it becomes proportionately slower, and as the total area of the channels diminishes again from the capillaries to the venæ cavæ, so does the rate of flow quicken, just as a river current slackens when it spreads out, and flows faster when it is confined to a narrower channel; a fact taken advantage of in the construction of Eads' jetties at the mouth of the Mississippi, the object of which is to make the water flow in a narrower channel and so with a more rapid current in that part of the river. Actual measurements as to the rate of flow in the arteries cannot be made on man, but from experiments on lower animals it is calculated that in the human carotid the blood flows about 500 millimeters (19.5 inches) in a second. In the capillaries the current travels only from 0.2 to 0.5 mm. ($\frac{1}{125}$ to $\frac{1}{50}$ inch) in a second. The average time taken by a portion of blood in making a complete circulation can easily be calculated if the output per heart-beat and the total quantity of blood in the Body are known; dividing the second figure by the first gives the number of heart-beats required to pass

all the blood in the Body through the heart once; if the pulse rate is known the time this will take, which equals the average time the blood takes in making a single complete round of the Body, is readily computed. Using 105 c. c. as the output per beat (p. 368), and 5,800 c. c. as the total blood volume (p. 320; there is a small error here since blood is a very little heavier than water, but the difference is too slight to matter), we obtain 55 as the number of heart-beats required, and at a rate of 70 beats per minute, a circulation time of 47 seconds.

This is, of course, purely an average figure; the circulation is made up of an enormous number of channels of widely varying length, so that the actual time taken by any given drop of blood may be considerably less or greater than that given above. The time required for blood to pass around the Body by the *shortest path* has been measured directly by injecting some easily detected substance into an artery on one side of the Body and noting the time which elapses before it can be found in a corresponding vein on the opposite side. In dogs this time is 15 seconds, and it is calculated for man at about 23 seconds. Of the total time from one to two and a half seconds are spent in the systemic capillaries and similar amounts of time in the pulmonary, as each portion of blood on its course from the last artery to the first vein passes through a length of capillary which on the average is 0.5 mm. ($\frac{1}{50}$ inch). The rate of flow in the great veins is about 100 mm. (4 inches) in a second, but is subject to considerable variations dependent on the respiratory and other movements of the Body; in the small veins it is much slower.

Secondary Factors Affecting the Circulation. While the heart's beat is the great driving force of the circulation, certain other things help more or less—viz., gravity, compression of the veins, and aspiration of the thorax. All of them are, however, quite subsidiary; experiment on the dead Body shows that the injection of defibrinated blood into the aorta under a less force than that exerted by the left ventricle during life is more than sufficient to drive it round and back by the venæ cavæ.

The Influence of Gravity. Under ordinary circumstances this may be neglected, since in parts of the Body below the level of the heart it will assist the flow in the arteries and impede it equally in the veins, while the reverse is the case in the upper parts of the

Body. In certain cases, however, it is well to bear these points in mind. A part "congested" or gorged with blood should if possible be raised so as to make the back-flow in its veins easier; and sometimes when the heart is acting feebly it may be able to drive blood along arteries in which gravity helps, but not otherwise. Accordingly in a tendency to fainting it is best to lie down, and make it easier for the heart to send blood up to the brain, deficiency in its blood-supply being the cause of the loss of consciousness in a fainting-fit. In fact, so long as the breathing continues, the aspiration of the thorax will keep up the venous flow (see below), while, in the circumstances supposed, a slight diminution in the resistance opposed to the arterial flow may be of importance. The head of a person who has fainted should accordingly never be raised until he has undoubtedly recovered, a fact rarely borne in mind by spectators, who commonly rush at once to lift any one whom they see fall in the street or elsewhere.

The Influence of Transient Compression of the Veins. The valves of the veins being so disposed as to permit only a flow towards the heart, when external pressure empties a vein it assists the circulation. Continuous pressure, as by a tight garter, is of course bad, since it checks all subsequent flow through the vessel; but intermittent pressure, such as is exerted on many veins by muscles in the ordinary movements of the Body, acts as a pump to force on the blood in them.

The value of this pumping of the blood out of the veins by muscular movements is well illustrated by comparing two classes of workers whose occupations require that they be upon their feet continuously for hours. The condition of *varicose veins*, which is a stasis of blood in the superficial veins of the lower extremities, is very prevalent among motormen, and others who must stand still for long periods, but is virtually unknown among postmen, who are walking during the time spent on their feet.

The valves of the veins have another use in diminishing the pressure on the lower part of those vessels in many regions. If, for instance, there were no valves in the long saphenous vein of the leg the considerable weight of the column of blood in it, which in the erect position would be about a meter (39 inches) high, would press on the lower part of the vessel. But each set of valves in it carries the weight of the column of blood between it and the

next set of valves above, and relieves parts below, and so the weight of the column of blood is distributed and does not all bear on any one point.

Aspiration of the Thorax (see also p. 420). Whenever a breath is drawn the pressure of the air on the vessels inside the chest is diminished, while that on the other vessels of the Body is unaffected. In consequence blood tends to flow into the chest. It cannot, however, flow back from the arteries on account of the semilunar valves of the aorta, but it can readily be pressed, or in common language "sucked," into the great veins close to the heart and into the right auricle of the latter. The details of this action must be omitted until the respiratory mechanism has been considered. All parts of the pulmonary circuit being within the thorax, the respiratory movements do not directly influence it, except in so far as the distention or collapse of the lungs alters the caliber of their vessels.

The considerable influence of the respiratory movements upon the venous circulation can be readily observed. In thin persons the jugular vein in the neck can often be seen to empty rapidly and collapse during inspiration, and fill up in a very noticeable way during expiration, exhibiting a sort of venous pulse. Every one, too, knows that by making a violent and prolonged expiration, as exhibited for example by a child with whooping cough, the flow in all the veins of the head and neck may be checked, causing them to swell up and hinder the capillary circulation until the person becomes "black in the face," from the engorgement of the small vessels with dark-colored venous blood.

Proofs of the Circulation of the Blood. The ancient physiologists believed that the movement of the blood was an ebb and flow, to and from each side of the heart, and out and in by both arteries and veins. They had no idea of a circulation, but thought pure blood was formed in the lungs and impure in the liver, and that these partially mixed in the heart through minute pores supposed to exist in the septum. Servetus, who was burnt alive by Calvin in 1553, first stated that there was a continuous passage through the lungs from the pulmonary artery to the pulmonary veins, but the great Englishman Harvey first, in lectures delivered in the College of Physicians of London about 1616, demonstrated that the movement of the blood was a continuous circulation as

we now know it, and so laid the foundation of modern Physiology. In his time, however, the capillary vessels had not been discovered, so that although he was quite certain that the blood got *somehow* from the final branches of the aorta to the radicles of the venous system, he did not exactly know *how*.

The proofs of the course of the circulation are at present absolutely conclusive, and may be summed up as follows: (1) Blood injected into an artery in the dead Body will return by a vein; but injected into a vein will not pass back by an artery. (2) The anatomical arrangement of the valves of the heart and of the veins shows that the blood can only flow *from* the heart, through the arteries and back *to* the heart by the veins. (3) A cut artery spurts from the end next the heart, a cut vein bleeds most from the end farthest from the heart. (4) A portion of a vein when emptied fills only from the end farthest from the heart. This observation can be made on the veins on the back of the hand of any thin person, especially if the vessels be first gorged by holding the hand in a dependent position for a few seconds. Select then a vein which runs for an inch or so without branching, place a finger on its distal end, and then empty it up to its next branch (where valves usually exist) by compressing it from below up. The vessel will then be found to remain empty as long as the finger is kept on its lower end, but to fill immediately when it is removed; which proves that the valves prevent any filling of the vein from its heart-end backwards. (5) If a bandage be placed around the arm, so as to close the superficial veins, but not tight enough to occlude the deeper-seated arteries, the veins on the distal side of the bandage will become gorged and those on its proximal side empty, showing again that the veins only receive blood from their ends turned towards the capillaries. (6) In the lower animals direct observation with the microscope shows the steady flow of blood from the arteries through the capillaries to the veins, but never in the opposite direction.

CHAPTER XXII

THE VASOMOTOR MECHANISM. DETAILS OF CAPILLARY BLOOD-FLOW. TRAUMATIC SHOCK. THE LYMPHATIC SYSTEM

The Distribution of Blood Among Various Parts of the Body. In the nervous control of the heart-beat we have, as already noted, a mechanism whereby the blood-flow through the Body as a whole can be modified in accordance with the needs of the organism. In the *vasomotor mechanism* we have an arrangement, equally important, whereby individual organs or regions can be furnished with a larger or smaller proportion of the whole circulation as their activities require. The significance of this *differential distribution* of blood becomes manifest when we note that the Body has not much more blood than just about enough to get along with, so that inactive tissues must be subject to depletion in order that the needs of active tissues can be met.

The Nerves of the Blood Vessels. The arteries, as already pointed out, possess a muscular coat composed of fibers arranged around them, so that their contraction can narrow the vessel. This coat is most prominent in the smaller vessels, the *arterioles*. These vascular muscles are under the control of certain special nerves called *vasomotor*, and these latter can thus govern the amount of blood reaching any organ at a given time. The vasomotor nerves belong to the autonomic system. Their physiology is therefore the application to special structures of the general principles laid down in connection with that system (Chap. XII).

In the heart we had to consider a rhythmically contracting organ the rate of whose contractions could be increased or diminished by the influence of extrinsic nerves; in the arteries, speaking broadly, we have to deal with muscle in a condition of tonic or constant contraction, which contraction can be increased by impulses coming through excitor or *vasoconstrictor* nerves, and diminished through the activity of inhibitory or *vasodilator* nerves. The general tonic contraction of the arterial muscle is, however, much more dependent on the vasoconstrictor nerve-fibers than is

the beat of the heart on the cardio-excitor nerves. The inhibitory (dilator) set of vasomotor nerves has a much less extensive distribution over the arterial system than the constrictor.

The Vasoconstrictor Nerves. If the ear of a white rabbit be held up against the light while the animal is kept quiet and not alarmed, the red central artery can be seen coursing along the translucent organ, giving off branches which by subdivision become too small to be separately visible, and the whole ear has a pink color and is warm from the abundant blood flowing through it. Attentive observation will show also that the caliber of the main artery is not constant; at somewhat irregular periods of a minute or more it dilates and contracts a little.

If the sympathetic trunk have been previously divided on the other side of the neck of the animal, the ear on that side will present a very different appearance. Its arteries will be much dilated and the whole ear fuller of blood, redder, and distinctly warmer; the slow alternating variations in arterial diameter also have disappeared. We get thus evidence that the normal mean caliber of the artery is maintained by influences reaching its muscular coat through the cervical sympathetic. Stimulation of the upper end of the cut nerve confirms this opinion. It is then seen that the arteries of the corresponding ear gradually contract until even the main vessel can hardly be seen, and in consequence the whole ear becomes pale and cold. After the stimulation is stopped the arteries again slowly dilate until they have regained their full paralytic size.

Quite similar phenomena can be observed in transparent parts of other living animals, as in the web of a frog's foot, the arteries of which dilate after section of the sciatic nerve and constrict when the peripheral end of the nerve is stimulated. In the case of other parts changes in temperature may be used to detect alterations in the flow of blood. In a dog or cat, for example, a sensitive thermometer placed between the toes indicates a rise of temperature, owing to increased flow of warm blood through the skin, after section of the chief nerve of the limb, and a fall of temperature (usually) during stimulation of the peripheral end of the divided nerve.

When the vasoconstrictor nerves cut are those controlling a large number of arteries, the dilation of the latter so much dimin-

ishes peripheral resistance to the blood-flow as to lead to a marked fall of general arterial pressure; and, due care being taken to avoid or to allow for concomitant variations in the rate or force of the heart's beat, this gives us another useful method of studying the distribution of the nerves concerned. For example, the *splanchnic nerves* are branches which spring from the thoracic portion of the sympathetic chain and pass through the diaphragm to end in the *solar plexus* from which nerves pass to the arteries of most of the abdominal viscera. The region whose blood vessels are innervated by these nerves is often spoken of as the *splanchnic* region. When the splanchnic nerves are cut on both sides arterial pressure falls enormously, from say 120 millimeters of mercury in the carotid of a dog to 15 or 20 millimeters, much of the blood of the Body lying almost stagnant in the dilated blood vessels of the abdomen. On the other hand, stimulation of the splanchnic nerves so diminishes the paths open for the circulation of the blood as to increase general blood-pressure greatly.

The skin and the abdominal organs seem to be the predominant localities of distribution of the vasoconstrictor nerves; other parts have them, but not in quantity sufficient to bring about any great general change in the blood-flow.

The Vasoconstrictor Center. This, one of the most important of the "vital" centers of the medulla, has not been identified anatomically with any particular group of nerve-cells, but its location is quite sharply defined physiologically. There is a small region of the medulla, known as the "vital knot," whose destruction is promptly fatal to the life of the organism. This region includes, in addition to at least one other "center," the vasoconstrictor center. From this center there is a constant outflow of impulses to all those arterioles of the Body whose muscles contain vasoconstrictor nerve-endings. This constant stream of constrictor impulses is the chief factor in the maintenance of so-called *vasomotor tone*, a condition of continuous moderate constriction of the arterioles by which general arterial pressure is kept at the proper level.

It is probable that the vasoconstrictor center consists physiologically of a number of associated centers which may act as a unit or separately. These "partial" centers are in connection with restricted vasomotor areas, and thus are enabled to bring about local vasomotor effects.

The Control of the Vasoconstrictor Center. This center, like the other "vital" centers of the medulla, is kept in activity in part reflexly, and in part, probably, through chemical stimulation brought by way of the blood. The whole stream of afferent impulses passing through the medulla plays upon it. Like the centers for controlling the heart-beat its activity may be increased through the influx of stimuli into it, or it may suffer depression for the same cause. We divide afferent impulses affecting the vasoconstrictor center, therefore, into two groups: those increasing its activity, *pressor* impulses, and those diminishing it, *depressor*-impulses. Certain sorts of stimuli are generally pressor in effect; pain, for example, usually brings about a reflex rise of blood-pressure through stimulating the vasoconstrictor center; cold on the skin acts similarly. It is possible that other stimuli may be pressor or depressor according to circumstances.

The Depressor Nerve. The best known nerve-tract which carries depressor impulses uniformly has already been mentioned. It is the afferent tract from the heart known, in animals where it is present as a separate trunk, as the *depressor* nerve. Stimulation of this nerve brings about, always, a reflex fall of blood-pressure, which is due mainly to vasodilation resulting from depression of the vasoconstrictor center. This nerve rises, not in heart tissue proper, but in the walls of the aorta near where that vessel springs from the heart and in the coronary arteries. An undue increase in blood-pressure, such as might affect the heart injuriously, subjects the aortic wall to unusual tension. This seems to stimulate receptors connecting with the depressor nerve mechanically. Thus the heart is protected against injury arising from working against too great resistance.

Vasodilator Nerves. We have already noticed, in connection with the control of the vasoconstrictor center, one method by which dilation of arterioles may be secured, namely, by inhibition of the tonic activity of vasoconstrictor fibers. Frequently, however, in the Body this is managed in another way; by efferent vasodilator nerves which inhibit, not the vasoconstrictor center, but the muscles of the blood vessels directly. The nerves of the skeletal muscles for example contain two sets of efferent fibers: one motor proper and the other vasodilator. When the muscle contracts in a reflex action or under the influence of the will both

sets of fibers are excited; so that when the organ is set at work its arteries are simultaneously dilated and more blood flows through it. But if the animal have previously administered to it such a dose of curare as just to throw out of function the true motor-fibers, stimulation of the nerve produces dilation of the arteries without a corresponding muscular contraction. Quite a similar thing occurs in the salivary glands. Their cells, which form the saliva, are aroused to activity by special nerve-fibers; but the gland-nerve also contains a quite distinct set of vasodilator fibers which normally cause a simultaneous dilation of the gland-artery, though either can be artificially stimulated by itself and produce its effect alone.

An interesting fact is that while the vasodilator nerves to the glands belong definitely to either the cranial or sacral subdivision of the autonomic system (parasympathetic nerves), those to the skeletal muscles and skin seem, on most careful study, to be actually sensory nerves which add to their function of conveying afferent impulses from receptors to center, that of conveying efferent vasodilator impulses to the small vessels of these regions. In addition to the histological evidence indicating this there is the fact that skin inflammation, as by croton oil or other irritant, does not occur if the *sensory* nerves to the region have been caused to degenerate, all other nerve trunks being left intact. This fact is important in its bearing on theories of nerve functioning (p. 171); it has little significance so far as vasodilator phenomena are concerned, since the efferent paths over these sensory nerves are presumably under the control of the dilator center, and function in harmony with the parasympathetic dilator pathways.

Since the effect of stimulating vasodilator nerves is the same as inhibiting the constrictor mechanism we might ask why there should be two distinct means thus provided for securing the same result. As a matter of fact the two mechanisms do not seem to overlap to any great extent; they rather supplement each other. The vasoconstrictor mechanism is confined, in the main, to the blood vessels of the skin and viscera; the dilator mechanism is distributed chiefly to the muscles, the glands, and the genital organs.

The effect of their combined action is well seen in vigorous muscular exercise when through splanchnic vasoconstriction

much blood that would otherwise flow through the viscera is diverted into other channels; by simultaneous vasodilation the vessels of the muscles become particularly available to receive this surplus flow; thus there is an automatic adjustment of the circulation to the metabolic requirements of the moment.

Through such arrangements the distribution of the blood in the Body is governed: so that working parts shall have abundance and other parts less. If the active region is relatively small; the muscles used in writing, for example; the general arterial pressure remains the same on the average; since the expansion of a few small local branches but little influences the total peripheral resistance in the vascular system. Moreover, as indicated above, when one set of organs is at work with its vessels dilated, others are at rest with their arteries comparatively contracted, and so a general average blood-pressure is maintained. Few persons feel inclined to do brain-work after a heavy meal; for then a greater part of the blood of the whole Body is led off into the dilated vessels of the digestive organs, and the brain gets a smaller supply.

The Vasodilator Center. There is reason to believe that the vasodilator nerves are under the control of a center in the medulla, which is in turn subject to the influence of afferent impulses of various sorts. The center is located about 3 mm. ($\frac{1}{10}$ inch) behind the vasoconstrictor center. So far as can be judged from observation of vasodilator phenomena the vasodilator center is probably not in constant tonic activity, as is the constrictor center, but is aroused to activity only when afferent stimuli come to it from certain particular regions.

The Relation of Vasomotor Tone to Cerebral Activity. The circulation through the brain differs in some important respects from that of the rest of the Body. The differences arise from the fact that the brain, a liquid and therefore incompressible mass, is inclosed in an unyielding receptacle, the skull, which it fills completely. The result is that the cerebral blood vessels occupy their allotted space, which cannot be either increased or diminished appreciably. The total volume of blood in the brain at any time is therefore practically constant, and the circulation through the brain can only be altered by changing the rate at which the blood flows through it. In such an arrangement as this, where local vasodilation cannot occur, the only way in which the rate of

blood-flow can be altered is by changes in the pressure at which the blood is forced into the region. The arteries feeding the brain spring directly from the aorta; it follows, therefore, that variations in aortic pressure, in other words, in general blood-pressure, are reflected exactly in the rate of cerebral blood-flow.

General blood-pressure, as we have seen, is maintained by vasomotor tone, the state of moderate constriction of arterioles generally. Variations in the tone of restricted areas, such as occur in connection with the functioning of individual organs, do not ordinarily affect general blood-pressure enough to alter the circulation through the brain to any extent.

There is good evidence that the degree of activity of the cells of the cerebral cortex is directly and immediately dependent upon the rate of blood-flow through the organ. A rapid circulation means alertness and efficiency of mental processes; as the flow becomes slower and slower the cells work less and less actively; when a certain point of sluggishness is reached consciousness disappears, the cells, if not altogether quiescent, working too feebly to arouse that state.

The phenomenon of fainting, which has already been mentioned, is the result usually of a sudden inhibition of the vasoconstrictor center whereby over a large area, the whole splanchnic region, for instance, there is general vasodilation and a resulting fall in blood-pressure. The rate of cerebral blood-flow falls to a point below that required for the maintenance of consciousness and the individual falls in a faint.

Sleep. This periodic loss of consciousness, so important for the proper restoration of the fatigued organs and tissues of the Body, has been the subject of considerable attention and investigation. Its explanation is not simple, involving as it does a number of questions, as, for instance, why fatigue, which ordinarily induces sleep, may, if extreme, prevent it; and what it is that causes one to awake after the proper number of hours of sleep.

Objectively sleep is marked by its well-known signs, which are not very instructive as to its cause, and also by certain vasomotor changes which have been looked upon as very instructive; and as affording us, indeed, our only satisfactory method of studying sleep experimentally. Observations upon sleeping individuals have shown that normal sleep is frequently accompanied by a

considerable fall in general blood-pressure, resulting from extensive vasodilation. This is itself sufficient to account for the diminished cerebral activity with its accompanying loss of consciousness which constitutes sleep, and many physiologists are inclined to believe, therefore, that the vasomotor changes may form the underlying basis for the phenomenon. A theory which expresses this view looks upon the vasoconstrictor center as the controlling mechanism of sleep. When this center is in good condition the constant stream of afferent impulses playing upon it maintains it in strong activity, and vasomotor tone is kept high. With the passage of hours of such ceaseless activity the center becomes fatigued and tends to respond less strongly to the afferent impulses coming to it. The result will be a falling off of vasomotor tone, unless by an effort of the will or an increase in the stream of afferent impulses, such as follows muscular exercise, for example, the center is whipped up to renewed activity. "Keeping awake" when one is sleepy is, according to this view, a matter of stimulating the tired vasoconstrictor center to continued effort. The effect may be produced by an artificial stimulant, such as coffee, or by an act of the will. The usual preparations for sleep are such as favor diminished activity of the vasoconstrictor center by lessening the afferent impulses coming to it. Lying in a comfortable position removes most of the impulses of muscle sense; by closing the eyes visual stimuli are got rid of. Thus unless the center is so irritable that the small stream of inevitable afferent impulses keeps it up to the mark the essential condition for sleep, loss of vasomotor tone, is fulfilled. The act of waking, according to this theory, results either from an undue stimulation of the vasoconstrictor center, as when one is waked by being violently shaken, or from a gradual restoration of the irritability of the center during its period of rest, to a point where the minimal stream of afferent impulses, inseparable from the living Body, is sufficient to stimulate it to the maintenance of waking vasomotor tone.

It must be admitted that not all experiments upon sleep have shown marked loss of vasomotor tone, and even if we consider vasomotor fatigue the primary factor we must grant, of course, that there are numerous additional factors modifying sleep. The condition of the cerebral cells, and the nature of their activity

doubtless have much to do with the phenomenon. These, however, are factors which physiology at present is unable to analyze completely, so that the vasomotor theory affords our most satisfactory explanation of sleep from the physiological standpoint.

Adrenin. The effect of this hormone upon the vascular system, as stated previously (Chap. XII), is to stimulate the vasoconstrictor fibers at their terminations in the muscles of the arterioles. The introduction of adrenin into the blood so much increases the constriction of the blood vessels in the skin and the splanchnic area as to produce a pronounced rise in blood-pressure, with a correspondingly augmented cerebral circulation. The same influence acts to divert the blood largely from skin and splanchnic regions to the skeletal muscles. The vessels of these latter being unprovided with vasoconstrictor fibers are not involved in the adrenin effect. Since the brain and the skeletal muscles are the regions specially in need of adequate nourishment in crises the significance of this reaction in time of emergency is obvious. The substance adrenin as used experimentally shows some striking characteristics. A very small concentration of it (one part in ten thousand), introduced into a capillary region, brings about so strong a constriction in the immediate neighborhood as to stop the flow of blood completely through that region. It is possible thus to prevent troublesome bleeding in small operations. The effect of adrenin used in this way is, however, very transient; repeated injections are necessary to maintain the constricted state.

Capillary Walls Independently Contractile. The control of the distribution of blood among the tissues as thus far described, depends on contractions and relaxations of the muscular walls of the arterioles under the influence of autonomic nerves. This mechanism is not, however, the sole agency involved; the capillaries themselves have a share in the work. It has been known for a long time that the walls of the capillaries can contract and relax; the action seems to be due in part to the Rouget cells found scattered along them (p. 353), although it is probable that the lining cells themselves (the tunica intima) have contractile power also. The evidence indicates that the vasomotor innervation to the arterioles extends also more or less effectively to the capillaries, so that the latter contract and relax in general harmony with the former. But in addition to this nervously controlled action the

capillaries have been shown recently to have a large measure of independent function, for which the regulation appears to come through chemical substances in the blood.

Capillaries Open and Close in Rotation. Methods have recently been devised whereby capillary fields can be observed directly under the microscope in the human skin and in various internal organs of such animals as frogs. The method as applied to the skin consists of first applying oil to the surface to make it semi-transparent and then bringing strong illumination to bear from the top or side, so that the capillaries can be seen below the surface. When a capillary area in a structure like a frog's muscle is observed over a period of time it is seen that under normal resting conditions only about ten per cent or so of the total number of capillaries in the field have blood flowing through them; the others are so constricted as not to be visible. Furthermore there is every now and then a shift from one set of capillaries to another; those that have been open, permitting blood to flow through them, close down, and a new set open out. The obvious conclusion is that the nutritive needs of resting cells are met without a continuous flow of blood through the capillaries adjacent to them. If blood flows for a short time, bringing needed food, oxygen, and hormones, and carrying off waste products and excess heat, it leaves the adjoining tissue fluids sufficiently replenished so that the cells dependent on them will not develop shortage immediately. Thus blood can be shunted for a time to other groups of capillaries without harm.

Pituitary Hormone (Posterior Lobe) Stimulates Capillaries to Close. On p. 59 the pituitary body is described as consisting of two lobes. The function of the anterior lobe is there discussed, but nothing is said as to the function of the other or posterior lobe. This lobe, which is an outgrowth downward from the base of the brain, appears to be wholly independent functionally of the anterior lobe, and to secrete a hormone (known as pituitrin) that has nothing to do with regulating growth, but serves to control the alternating closing and opening of the capillaries. The action of the hormone seems to be simply that of stimulating capillaries to close whenever it is brought in contact with their walls by being present in the blood flowing through them. The hormone may be opposed by other influences present at the same time which tend to cause

the capillary walls to relax, so that it is not necessary to assume that capillaries will always close the instant pituitrin-containing blood enters them. We can construct a picture of the mechanism for opening and closing the capillaries in rotation, something as follows: starting with a capillary that is open, blood is flowing through it and by interchange with the adjacent tissue fluids is affording the surrounding cells abundant nourishment; the blood contains pituitrin, however, poured into it from the gland (posterior lobe) which produces the hormone, hence the capillary will presently be stimulated to constrict, and so shut off the flow of blood through itself; as soon as this happens the influence of the pituitrin begins to wane, since none is now reaching the capillary walls, and at the same time the adjacent tissue fluids begin to be depleted of oxygen and other materials by the surrounding cells, and to become charged with waste products. It is probable that these latter act as stimuli to cause the capillary walls to dilate; at any rate in course of time the closure gives place to opening, and the cycle starts once more. The number of capillaries in any given tissue is so large that all the possible stages of this process are likely to be going on simultaneously; thus the rotation of function among the capillaries occurs.

In Active Tissues all Capillaries Open Widely. We have already seen that through the operation of the vasomotor mechanism the blood supply of active tissues is improved at the expense of inactive (p. 396). Hand in hand with this shunting of the whole current of blood toward active regions goes a general opening out of the capillaries in them. Presumably the cause of this is the great increase in quantity of waste products formed by the active tissues; thus in spite of the continuous presence of pituitrin the capillaries remain open, the dilating effect of the abundant waste substances overcoming the constricting influence of the hormone. The effect is obviously to facilitate materially the interchanges between blood and tissue fluids. During activity these are continuous instead of taking place only at such intervals as the opening of individual capillaries in their turn allows.

Filtration more Copious the more Widely are the Capillaries Dilated. In any open capillary there is necessarily a conflict of stimulation between the waste products tending to keep it dilated and the pituitrin tending to constrict it. It follows that the capil-

lary may be more widely open at one time than at another, according as one or the other influence gains ascendency. This possibility has taken on great significance as the result of the recent discovery that the blood-plasma filters through the walls of widely dilated capillaries much more freely than through the walls of those that are less dilated. It will be recalled that the fluid in the tissue spaces owes its origin to blood-plasma that filters out thus (p. 308), as does also the lymph in the lymphatic vessels.

Special Capillary Dilators: Histamine. During the Great War the discovery was made that certain organic substances, notably *histamine*, a derivative of one of the amino-acids present in body-proteins, are much more effective as capillary dilators than the ordinary waste products of metabolism. When such compounds are injected into the circulation they cause all the capillaries in the Body to open out widely. The effect is disastrous. In the first place with all the capillaries dilated so large a percentage of all the blood in the Body is in them that not enough remains in the large vessels to maintain an adequate circulation. The great veins have only a fraction as much blood in them as normal; the heart therefore is poorly filled, and so pumps less blood out into the large arteries. Arterial pressure falls, cutting down the circulation through the brain. The ill effect is emphasized by the increased escape of plasma by filtration from the widely dilated capillaries, cutting down still further the quantity of fluid in circulation.

Traumatic Shock. Individuals who suffer injuries involving severe tissue laceration frequently go into a state of collapse known as *shock* (note that "shell shock" is an entirely different phenomenon of central nervous origin). The symptoms are such as to indicate that the circulation is inadequate, and the method of treatment is to endeavor to restore the circulation. The cause of traumatic shock, *i. e.*, shock due to *trauma* or tissue injury, remained a mystery until the discovery described in the paragraph above. Following up the suggestion contained therein it was found that lacerated tissues, as they decompose, give off into the blood decomposition products that have a histamine-like action on the capillary walls. It is possible that histamine itself is formed, although this seems not to have been proven as yet. At any rate we have in this poisoning of the Body by decomposition products of injured tissues an

explanation of traumatic shock, whether caused by wounds, "wound shock," or by severe surgical operations, "surgical shock." It also appears that the profound depression and slow recovery following severe burns are similarly caused.

The Lymphatic System. We have already seen (p. 310) that the tissue fluids as they tend to accumulate by filtration of blood-plasma into the tissue spaces are drained away from the tissues and carried back to the blood. This drainage is afforded by the *lymphatic system.* At its beginning this system consists of minute vessels having definite although excessively delicate walls. These are the beginnings of definite lymph-channels.

The Structure of Lymph-Vessels. The smallest lymph-vessels proper are the *lymph-capillaries;* tubes rather wider than the blood-capillaries, but like them having a wall consisting of a single layer of flattened epithelium cells. The cells have, however, a wavy margin and are not as a rule much longer in one diameter than another, in both of which respects they differ from the cells of the corresponding blood vessels. In some regions, as in many glands, the lymph-capillaries are much dilated and from irregular lymph *lacunæ,* everywhere bounded by their peculiar wavy cells, lying in the interstices of organs; and sometimes they form tubes around small blood vessels, as in the brain (*perivascular lymph-channel*). In some places they commence by blind ends as in the lacteal vessels of the villi of the small intestine (Fig. 131) which are lymph-capillaries; but usually they branch and join to form networks. Fluid from the intercellular spaces enters them by filtering through their boundary cells and is passed on to larger vessels which much resemble veins of corresponding size, having the same three coats, and being abundantly provided with valves.

The Thoracic Duct. The lymph-vessels proceeding from the capillaries in various organs become larger and fewer by joining together, and all end finally in two main trunks which open into the venous system on the sides of the neck, at the point of junction of the jugular and subclavian veins. The trunk on the right side is much smaller than the other and is known as the "*right lymphatic duct.*" It collects lymph from the right side of the thorax, from the right side of the head and neck, and the right arm. The lymph from all the rest of the Body is collected into the *thoracic duct.* It commences at the upper part of the abdominal cavity

in a dilated reservoir (the *receptaculum chyli*), into which the lacteals from the intestines, and the lymphatics of the rest of the lower part of the Body, open. From thence the thoracic duct, receiving tributaries on its course, runs up the thorax alongside of the aorta and, passing on into the neck, ends on the left side at the point already indicated; receiving on its way the main stems from the left arm and the left side of the head and neck. The thoracic duct, thus, brings back to the blood much more lymph than the right lymphatic duct.

Lymph-Nodes. At intervals along the course of various lymphatic vessels are structures consisting of cells so arranged as to leave interspaces among them, through which interspaces the lymph is forced to flow. These structures are the *lymph-nodes* or *lymph-glands* and the peculiar tissue of which they are composed is *lymphoid* or *adenoid* tissue. Lymph-nodes occur in the neck, the groin, the axilla (armpit) and in various other regions of the Body. Certain structures in the wall of the small intestine near its lower end, the so-called *Peyer's Patches*, are composed of lymphoid tissue as are also the structures in the throat making up the *tonsilar ring*.

Functions of Lymph-Nodes. Two quite different functions are attributed to the lymph-nodes. The first of these is that previously mentioned (p. 317) of serving as the seat of lymphocyte production.

The lymph-nodes have also the additional function of filtering the lymph that passes through them. This filtering action is probably of great importance in confining micro-organisms to the region which they first enter, since if they get into the lymph-stream they are arrested at the first lymph-node. It is thought that the lymph-nodes are able also to arrest, for a time at least, the spread of cancer-cells over the Body. The lymph-nodes located on the channels draining the lungs become filled with dust that has worked its way through the pulmonary walls into the lymph, and is prevented thus from spreading throughout the Body.

Tonsils and Adenoids. The irregular ring of lymphoid tissue surrounding the throat was referred to above. This at the front shows two enlargements, one on each side, known as the *tonsils*. At the back of the throat this same ring often in children becomes enlarged by overgrowth until it obstructs the nasal passage and

interferes with the breathing. It may also obstruct the Eustachian tubes and cause partial deafness. This overgrowth is known as *adenoids*. The removal of adenoids is a simple matter surgically, and is advisable wherever there is evident obstruction of the breathing.

The tonsils, which function in the manner of lymphoid tissue generally, to filter out organisms from the lymph-stream, are peculiarly liable to invasion by the organisms of common colds and also by those which form pus (*staphylococcus* and *streptococcus*). When any of these become established in the tonsils and set up inflammation therein the very painful condition called *tonsilitis* results. In many cases the tonsils become permanently infected. In such there is a steady production of toxins which are discharged into the lymph-stream and thence pervade the Body. Malnutrition in children and adults is often to be accounted for solely on the basis of chronic poisoning from infected tonsils. There is also reason to believe that acute rheumatism is caused similarly. In such cases the possible good that may come to the Body from the normal functioning of the tonsils is so far outweighed by the harm they do as seats of infection that they should obviously be removed.

The Movement of the Lymph. This is no doubt somewhat irregular in the commencing vessels, but, on the whole, sets on to the larger trunks and through them to the veins. In many animals (as the frog) at points where the lymphatics communicate with the veins, there are found regularly contractile "lymph-hearts" which beat with a rhythm independent of that of the blood-heart, and pump the lymph into a vein. In the Human Body, however, there are no such hearts, and the flow of the lymph is dependent on less definite arrangements. It seems to be maintained mainly by three things: (1) The pressure on the blood-plasma in the capillaries is greater than that in the great veins of the neck; hence any plasma filtered through the capillary-walls will be under a pressure which will tend to make it flow to the venous termination of the thoracic or the right lymphatic duct. (2) On account of the numerous valves in the lymphatic vessels (which all only allow the lymph to flow past them to larger trunks) any movement compressing a lymph-vessel will cause an onward flow of its contents. The influence thus exerted

is very important. If a tube be put in a large lymphatic, say at the top of the leg of an animal, it will be seen that the lymph only flows out very slowly while the animal is quiet; but as soon as it moves the leg the flow is greatly accelerated. (3) During each inspiration the pressure on the thoracic duct is less than that in the lymphatics in parts of the Body outside the thorax (see Chap. XXIII). Accordingly, at that time, lymph is pressed, or, in common phrase, is "sucked," into the thoracic duct. During the succeeding expiration the pressure on the thoracic duct becomes greater again, and some of its contents are pressed out; but on account of the valves of the vessels which unite to form the duct, they can only go towards the veins of the neck.

During digestion, moreover, contractions of the villi and of the intestinal walls press on the lymph or chyle within them and force it on; and in certain parts of the Body gravity, of course, aids the flow, though it will impede it in others.

The Action of Lymphagogues. Any substance that causes a pronounced increase in the rate of lymph formation is known as a *lymphagogue.* The source of lymph, we have already seen (p. 309), is in the main by filtration through the capillary walls. Evidently lymphagogues act by increasing this filtration. There are two ways in which this might be brought about, and lymphagogues are assigned to one of two classes according to which of the ways they use. The first is by making the capillary walls more permeable, and so increasing the outpouring of lymph. Substances which have this effect are shell fish, strawberries, some meat extracts, egg-white and related organic compounds. Not all people are affected by these lymphagogues. Nor are those that are susceptible to one necessarily susceptible to all. Where the capillaries whose permeability is increased are superficial the outpouring lymph forms blotches on the skin. The condition is known as *urticaria* or *hives.* Mechanical injury to the capillaries may cause a similar outpouring, as seen in the swelling from a bruise.

The second method of increasing the flow of lymph is by producing an engorgement of the capillaries, a condition known as *hydremic plethora.* This can be brought about by raising the osmotic pressure of the blood, as by injecting into it a strong sugar solution. The effect is to cause a rush of tissue fluid into

the blood through the capillary-walls. It has been shown that in this situation the plethora is relieved chiefly by an increased filtration through the capillaries of the liver. The conclusion is drawn that these are the most permeable in the Body. The lymph thus formed passes to the thoracic duct and back to the blood, so that evidently no permanent advantage is gained. The excess of fluid is finally discharged through the kidneys.

CHAPTER XXIII

RESPIRATION. THE MECHANISM OF BREATHING. THE REGULATION OF BREATHING

Definitions. The blood as it flows from the right ventricle of the heart, through the lungs, to the left auricle, loses carbon dioxid and gains oxygen. In the systemic circulation exactly the reverse changes take place, oxygen leaving the blood to supply the living tissues; and carbon dioxid, generated in them, passing back into the blood capillaries. The oxygen loss and carbon dioxid gain are associated with a change in the color of the blood from bright scarlet to purple-red, or from arterial to venous; and the opposite changes in the lungs restore to the dark blood its bright tint. The whole set of processes through which blood becomes venous in the systemic circulation and arterial in the pulmonary—in other words, the processes concerned in the gaseous reception, distribution, and elimination of the Body—constitute the function of *respiration;* so much of this as is concerned in the interchanges between the blood and air being known as *external respiration;* while the interchanges occurring between the tissues and the systemic capillaries through the lymph, constitute *internal respiration.* When the term respiration is used alone, without any limiting adjective, the external respiration only, is commonly meant.

Respiratory Organs. The blood being kept poor in oxygen and rich in carbon dioxid by the action of the living tissues, a certain amount of gaseous interchange will nearly always take place when it comes into close proximity to the surrounding medium; whether this be the atmosphere itself or water containing air in solution. When an animal is small there are often no special organs for its external respiration, its general surface being sufficient (especially in aquatic animals with a moist skin) to permit of all the gaseous exchange that is necessary. In the simplest creatures, indeed, there is even no blood, the cell or cells composing them taking up for themselves from their environment the oxygen which they need, and passing out into it their carbon dioxid waste; in other words, there is no differentiation of the external and inter-

nal respirations. When, however, an animal is larger many of its cells are so far from a free surface that they cannot transact this give-and-take with the surrounding medium directly, and the blood, or some liquid representing it in this respect, serves as a middleman between the living tissues and the external oxygen; and then one usually finds special *respiratory organs* developed, to which the blood is brought to make good its oxygen loss and get rid of its excess of carbon dioxid. In aquatic animals such organs take commonly the form of gills; these are protrusions of the body over which a constant current of water, containing oxygen in solution, is kept up; and in which blood capillaries form a close network immediately beneath the surface. In air-breathing animals a different arrangement is usually found. In some, as frogs, it is true, the skin is always moist and serves as an important respiratory organ, large quantities of venous blood being sent to it for aëration. But for the occurrence of the necessary gaseous diffusion, the skin must be kept very moist, and this, in a terrestrial animal, necessitates a great amount of secretion by the cutaneous glands to compensate for evaporation; accordingly in most land animals the air is carried into the body through tubes with narrow external orifices and so the drying up of the breathing surfaces is greatly diminished; just as water in a bottle with a narrow neck will evaporate much more slowly than the same amount exposed in an open dish. In insects (as bees, butterflies, and beetles) the air is carried by tubes which split up into extremely fine branches and ramify all through the Body, even down to the individual tissue elements, which thus carry on their gaseous exchanges without the intervention of blood. But in the great majority of air-breathing animals the arrangement is different; the air-tubes leading from the exterior of the Body do not subdivide into branches which ramify all through it, but open into one or more large sacs to which the venous blood is brought, and in whose walls it flows through a close capillary network. Such respiratory sacs are called *lungs*, and it is a highly developed form of them which is found in the Human Body.

The Air-Passages and Lungs. In our own Bodies the essential gaseous interchanges between the Body and the atmosphere take place in the lungs, two large sacs (*lu*, Fig. 1) lying in the thoracic cavity, one on each side of the heart. To these sacs the air is

conveyed through a series of passages. Entering the pharynx through the nostrils or mouth, it passes out of this by the opening leading into the larynx, or voice-box (*a*, Fig. 118), lying in the upper part of the neck (the communication of the two is seen in Fig. 128); from the larynx passes back the *trachea* or windpipe, *b*, which, after entering the chest cavity, divides into the *right* and *left bronchi*, *d*, *e*. Each bronchus divides up into smaller and smaller branches, called *bronchial tubes*, within the lung on its own side; and the smallest bronchial tubes end in sacculated dilations, the *infundibula* of the lungs, the sacculations (Fig. 120) being the *alveoli*. On the walls of the alveoli the pulmonary capillaries ramify, and it is in them that the interchanges of the external respiration take place.

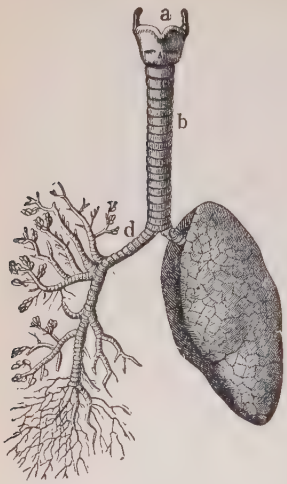


FIG. 118.—The lungs and air-passages seen from the front. On the left of the figure the pulmonary tissue has been dissected away to show the ramifications of the bronchial tubes. *a*, larynx; *b*, trachea; *d*, right bronchus. The left bronchus is seen entering the *root* of its lung.

Structure of the Trachea and Bronchi. The windpipe may readily be felt in the middle line of the neck, a little below Adam's apple, as a rigid cylindrical mass. It consists fundamentally of a fibrous tube in which cartilages are imbedded, so as to keep it from collapsing; and is lined internally by a mucous membrane covered by several layers of epithelial cells, of which the superficial is ciliated. The elastic cartilages imbedded in its walls are imperfect rings, each somewhat the shape of a horseshoe and the deficient part of each ring being turned backwards, it comes to pass that the deeper or dorsal side of the windpipe has no hard parts in it. Here the wall consists of smooth muscle. Against this the gullet lies, the absence of cartilage facilitating swallowing. The bronchi are similar in structure.

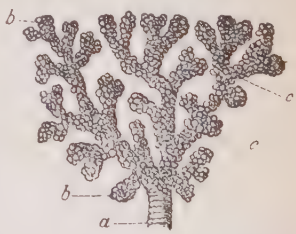


FIG. 119.—A small bronchial tube, *a*, dividing into its terminal branches, *c*; these have pouched or sacculated walls and end in the sacculated infundibula, *b*.

The Structure of the Lungs. These consist of the bronchial tubes and their terminal dilations; numerous blood vessels, nerves, and lymphatics; and an abundance of connective tissue, rich in elastic fibers, binding all together. The bronchial tubes ramify in a tree-like manner (Fig. 118). The larger ones resemble the trachea, except that the cartilage rings do not have their open parts all turned one way, and the smooth muscle encircles the tube completely. As the tubes become smaller their constituents thin away; the cartilages become less frequent and finally disappear; the epithelium is reduced to a single layer of cells which, though still ciliated, are much shorter than the columnar superficial cell-layer of the larger tubes. The terminal alveoli (*b*, Fig. 120) have walls composed mainly of elastic tissue and lined by a single layer of flat, nonciliated epithelium, immediately beneath which is a very close network of capillary blood vessels. The air entering by the bronchial tube is thus only separated from the blood by the thin capillary wall and the thin epithelium, both of which are moist, and well fitted for gaseous diffusion.

FIG. 120.—Two infundibula of the lung much magnified. *b*, *b*, hollow protrusions of the alveolus, opening into its central cavity; *c*, terminal branches of a bronchial tube.

The Pleura. Each lung is covered, except at one point, by an elastic serous membrane which adheres tightly to it and is called the *pleura;* that point at which the pleura is wanting is called the *root* of the lung and is on its median side; it is there that its bronchus, blood vessels and nerves enter it. At the root of the lung the pleura turns back and lines the inside of the chest cavity, as represented by the heavy black line in the diagram Fig. 3. The part of the pleura attached to each lung is its *visceral,* and that attached to the chest-wall its *parietal layer.* Each pleura thus forms a closed sac surrounding a *pleural cavity,* in which, during health, there are found a few drops of fluid, keeping its surfaces moist. This lessens friction between the two layers during the movements of the chest-walls and the lungs; for although, to insure distinctness, the visceral and parietal layers of the pleura

are represented in the diagram as not in contact, that is not the natural condition of things; the lungs are in life distended so that the visceral pleura rubs against the parietal, and the pleural cavity is practically obliterated. This is due to the pressure of the atmosphere exerted through the air-passages on the interior of the lungs. The lungs are extremely elastic and distensible, and when the chest cavity is perforated each shrivels up just as a rubber balloon does when its neck is opened; the reason being that then the air presses on the outside of each with as much force as it does on the inside. These two pressures neutralizing one another, there is nothing to overcome the tendency of the lungs to collapse. So long as the chest-walls are whole, however, the lungs remain distended. The pleural sac is air-tight and contains no air, and the pressure of the air around the Body is borne by the rigid walls of the chest and prevented from reaching the lungs; consequently no atmospheric pressure is exerted on their outside. On their interior, however, the atmosphere presses with its full weight, equal to about 90 centigrams on a square centimeter (14.5 lbs. on the square inch), and this is far more than sufficient to distend the lungs so as to make them completely fill all the parts of the thoracic cavity not occupied by other organs. Suppose *A* (Fig. 121) to be a bottle closed air-tight by a cork through which two tubes pass, one of which, *b*, leads into an elastic bag, *d*, and the other, *c*, provided with a stopcock, opens freely below into the bottle. When the stopcock, *c*, is open the air will enter the bottle and press there on the outside of the bag, as well as on its inside through *b*. The bag will therefore collapse, as the lungs do when the chest cavity is opened. But if some air be sucked out through *c* the pressure of that remaining in the bottle will diminish, and of that inside the bag will be unchanged, and the bag will thus be blown up, because the atmospheric pressure on its interior will not be balanced by that on its exterior. At last, when all the air is sucked out of the bottle and the stopcock on *c* closed, the bag, if sufficiently distensible, will be expanded so as to completely fill the bottle and press against its inside, and the state of things will then answer to that naturally found in the chest. If the bottle

FIG. 121. — Diagram illustrating the pressure relationships of the lungs in the thorax.

were now increased in size without letting air into it, the bag would expand still more, so as to fill it, and in so doing would receive air from outside through *b*; and if the bottle then returned to its original size, its walls would press on the bag and cause it to shrink and expel some of its air through *b*. Exactly the same must of course happen, under similar circumstances, in the chest, the windpipe answering to the tube *b* through which air enters or leaves this elastic sac.

The Breathing Movements. The air taken into the lungs soon becomes laden in them with carbon dioxid, and at the same time loses much of its oxygen; these interchanges take place mainly in the deep recesses of the alveoli, far from the exterior and only communicating with it through a long tract of narrow tubes. The alveolar air could be renewed slowly by gaseous diffusion with the atmosphere through the long air-passages it is true, but not fast enough even for the requirements of the resting Body, as one learns by the sensation of suffocation which follows holding the breath for a short time with mouth and larynx open, and far from quickly enough to meet the greatly increased requirements of the Body in activity. To insure adequate renewal of the alveolar air under all conditions of bodily activity there is a mechanism for *positive lung ventilation*, by which the air within the alveoli is periodically mixed with fresh air taken from the outside. This mixing is brought about by the breathing movements, consisting of regularly alternating *inspirations*, during which the chest cavity is enlarged and fresh air enters the lungs, and *expirations*, in which the cavity is diminished and air expelled from the lungs. When the chest is enlarged the air the lungs contain immediately distends them so as to fill the larger space; in so doing it becomes rarefied and less dense than the external air; and since gases flow from points of greater to those of less pressure, some outside air at once flows in by the air-passages and enters the lungs. In expiration the reverse takes place. The chest cavity, diminishing, presses on the lungs and makes the air inside them denser than the external air, and so some passes out until an equilibrium of pressure is restored. The chest, in fact, acts very much like a bellows. When the bellows are opened air enters in consequence of the rarefaction of that in the interior, which is expanding to fill the larger space, and when the bellows are closed again it is expelled. To make

the bellows quite like the lungs we must, however, as in Fig. 122, have only one opening in them, that of the nozzle, for both the entry and exit of the air; and this opening should lead, not directly into the bellows-cavity, but into an elastic bag lying in it, and tied to the inner end of the nozzle-pipe. This sac would represent the lungs and the space between its outside and the inside of the bellows, the pleural cavities.

Fig. 122.—Diagram to illustrate the entry of air to the lungs when the thoracic cavity enlarges.

We have next to see how the expansion and contraction of the chest cavity are brought about.

The Structure of the Thorax. The thoracic cavity has a somewhat conical form determined by the shape of its skeleton (Fig. 123), its narrower end being turned upwards. Dorsally, ventrally, and on the sides, it is supported by the rigid framework afforded by the thoracic vertebræ, the breastbone, and the ribs. Between and

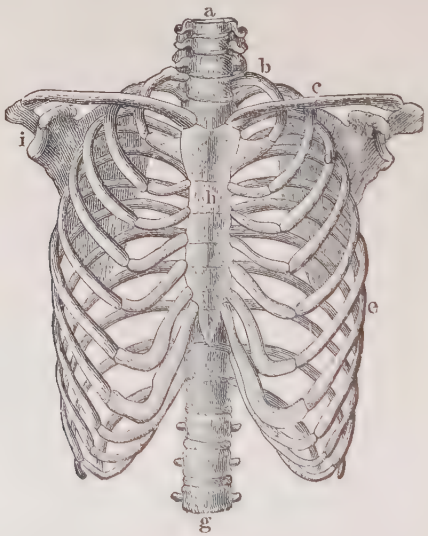


Fig. 123.—The skeleton of the thorax. *a*, *g*, vertebral column; *b*, first rib; *c*, clavicle; *e*, seventh rib; *i*, glenoid fossa.

over these lie muscles, and the whole is covered in, air-tight, by the skin externally, and the parietal layers of the pleuræ inside. Above, its aperture is closed by muscles and by various organs

passing between the thorax and the neck; and below it is bounded by the *diaphragm*, which forms a movable bottom to the, otherwise, tolerably rigid box. In inspiration this box is increased in all its diameters—dorsiventrally, laterally, and from above down.

The Vertical Enlargement of the Thorax. This is brought about by the contraction of the diaphragm which (Figs. 1 and 124) is a thin muscular sheet, with a fibrous membrane, serving as a tendon, in its center. In rest, the diaphragm is dome-shaped, with its concavity towards the abdomen, being supported in that position by the pressure of the underlying abdominal organs.

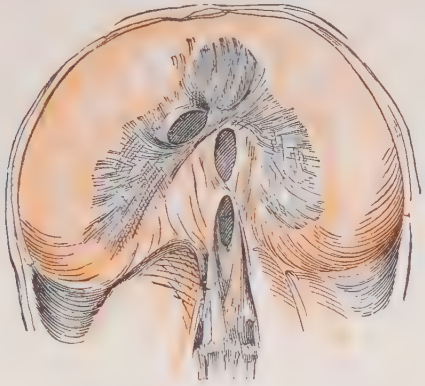


FIG. 124.—The diaphragm seen from below.

From the tendon on the crown of the dome striped muscular fibers radiate, downwards and outwards, to all sides; and are fixed by their outer ends to the lower ribs, the breastbone, and the vertebral column. In expiration the lower lateral portions of the diaphragm lie close against the chest-walls, no lung intervening between them. In inspiration the muscular fibers, shortening, flatten the dome and enlarge the thoracic cavity, room for the viscera thus displaced being secured by stretching the abdominal walls; at the same time its lateral portions are pulled away from the chest-walls, leaving a space into which the lower ends of the lungs expand. The contraction of the diaphragm thus increases greatly the size of the thorax chamber by adding to its lowest and widest part.

The Dorsiventral Enlargement of the Thorax. The ribs on the whole slope downwards from the vertebral column to the breastbone, the slope being most marked in the lower ones. During inspiration the breastbone and the sternal ends of the ribs attached to it are raised, and so the distance between the sternum and the vertebral column is increased. That this must be so will readily be seen on considering the diagram Fig. 125, where *ab*

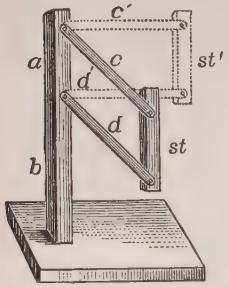


FIG. 125.—Diagram illustrating the dorsiventral increase in the diameter of the thorax when the ribs are raised.

represents the vertebral column, *c* and *d* two ribs, and *st* the sternum. The continuous lines represent the natural position of the ribs at rest in expiration, and the dotted lines the position in inspiration. It is clear that when their lower ends are raised, so as to make the bars lie in a more horizontal plane, the sternum is pushed away from the spine, and so the chest cavity is increased dorsiventrally. The inspiratory elevation of the ribs is mainly due to the action of the *scalene* and *external intercostal muscles*. The scalene muscles, three on each side, arise from the cervical vertebræ, and are inserted into the upper ribs. The external intercostals (Fig. 126, *A*) lie between the ribs and extend from the vertebral column to the costal cartilages; their fibers slope down-

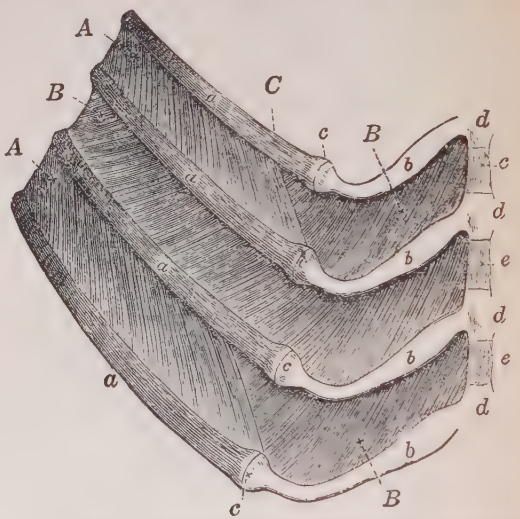


FIG. 126.—Portions of four ribs of a dog with the muscles between them. *a, a*, ventral ends of the ribs, joining at *c* the rib cartilages, *b*, which are fixed to cartilaginous portions, *d*, of the sternum. *A*, external intercostal muscle, ceasing between the rib cartilages, where the internal intercostal, *B*, is seen. Between the middle two ribs the external intercostal muscle has been dissected away, so as to display the internal which was covered by it.

wards and forwards. During an inspiration the scalenes contract and fix the upper ribs firmly; then the external intercostals shorten and each raises the rib below it. The muscle, in fact, tends to pull together the pair of ribs between which it lies, but as the upper one of these is held tight by the scalenes and other muscles above, the result is that the lower rib is pulled up, and not the upper down. In this way the lower ribs are raised much more than the upper, for the whole external intercostal muscles on each side may be regarded as one great muscle with many bellies, each belly separated from the next by a tendon, represented by the rib. When the whole muscular sheet is fixed above and contracts, it is clear that its lower end will be raised more than any intermediate point, since there is a greater length of contracting muscle above it. The elevation of the ribs tends to diminish the vertical diameter of the chest; this is more than compensated for by the simultaneous descent of the diaphragm.

The Lateral Enlargement of the Chest is brought about by a rotation of the middle ribs which, as they are raised, roll round a little at their vertebral articulations and twist their cartilages. Each rib is curved and, if the bones be examined in their natural position in a skeleton, it will be seen that the most curved part lies below the level of a straight line drawn from the vertebral to the sternal attachment of the bone. By the rotation of the rib, during inspiration, this curved part is raised and turned out, and the chest widened. The mechanism can be understood by clasping the hands opposite the lower end of the sternum and a few inches in front of it, with the elbows bent and pointing downwards. Each arm will then answer, in an exaggerated way, to a curved rib, and the clasped hands to the breastbone. If the hands be simply raised a few inches by movement at the shoulder-joints only, they will be separated farther from the front of the Body, and rib elevation and the consequent dorsiventral enlargement of the cavity surrounded will be represented. But if, simultaneously, the arms be rotated at the shoulder-joints so as to raise the elbows and turn them out a little, it will be seen that the space surrounded by the two arms is considerably increased from side to side, as the chest cavity is in inspiration by the similar elevation of the most curved part or "angle" of the middle ribs.

Expiration. To produce an inspiration requires considerable muscular effort. The ribs and sternum have to be raised; the elastic rib cartilages bent and somewhat twisted; the abdominal viscera pushed down; and the abdominal wall pushed out to make room for them. In ordinary expiration, on the contrary, no muscular effort is needed. As soon as the muscles which have raised the ribs and sternum relax, these tend to return to their natural unconstrained position, and the rib cartilages, also, to untwist themselves and bring the ribs back to their position of rest; the elastic abdominal wall presses the contained viscera against the underside of the diaphragm, and pushes that up again as soon as its muscular fibers cease contracting. By these means the chest cavity is restored to its original capacity and the air forced out of the lungs, by the elasticity of the parts which were stretched or twisted in inspiration, and not by any special expiratory muscles.

Forced Respiration. When a very deep breath is drawn or expelled, or when there is some impediment to the entry or exit of the air, a great many muscles take part in producing the respiratory movements; and expiration then becomes, in part, an actively muscular act. The main expiratory muscles are the *internal intercostals* which lie beneath the external between each pair of ribs (Fig. 126, *B*), and have an opposite direction, their fibers running upwards and forwards. In forced expiration the lower ribs are fixed or pulled down by muscles running in the abdominal wall from the pelvis to them and to the breastbone. The internal intercostals, contracting, pull down the upper ribs and the sternum, and so diminish the thoracic cavity dorsiventrally. At the same time, the abdominal muscles contract and press the walls of that cavity against the viscera within it, pushing these up forcibly against the diaphragm. This is thus made very convex towards the chest, diminishing the latter in its vertical diameter. In very violent expiration many other muscles may co-operate, tending to fix points on which those muscles which can directly diminish the thoracic cavity, pull. In violent inspiration, also, many extra muscles are called into play. The neck is held rigid to give the scalenes a firm attachment; the shoulder-joint is held fixed and muscles going from it to the chest-wall, and commonly serving to move the arm, are then used to elevate the ribs; the head is held firm on the vertebral column by the muscles

going between the two, and then other muscles, which pass from the collar bone and sternum to the skull, are used to pull up the former. The muscles which are thus called into play in labored but not in quiet breathing are called *accessory muscles of respiration.*

The Respiratory Sounds. The entry and exit of air are accompanied by *respiratory sounds* or *murmurs,* which can be heard on applying the ear to the chest-wall. The character of these sounds is different and characteristic over the trachea, the larger bronchial tubes, and portions of lung from which large bronchial tubes are absent. They are variously modified in pulmonary affections, and hence the value of *auscultation* of the lungs in assisting the physician to form a diagnosis.

The Capacity of the Lungs. Since the chest cavity never even approximately collapses, the lungs are never completely emptied of air: the space they have to occupy is larger in inspiration than during expiration, but is always considerable, so that after a forced expiration they still contain a large amount of air which can only be expelled from them by opening the pleural cavities; then they collapse almost completely, retaining within them only a small quantity of air imprisoned within the alveoli by the collapse of the small bronchi.

The capacity of the chest, and therefore of the lungs, varies much in different individuals, but in a man of medium height there remain in the lungs after the most violent possible expiration, about 1,000 cubic centimeters of air, called the *residual air.* After an ordinary expiration there will be in addition to this about 1,600 c. c. of *supplemental air;* the residual and supplemental together forming the *stationary air,* which remains in the chest during quiet breathing. In an ordinary inspiration 500 c. c. (30 cub. inches) of *tidal air* are taken in, and about the same amount is expelled in natural expiration. By a forced inspiration about 1,600 c. c. (98 cub. inches) of *complemental air* can be added to the tidal air. After a forced inspiration, therefore, the chest will contain $1,000 + 1,600 + 500 + 1,600 = 4,700$ c. c. (300 cub. inches) of air. The amount which can be taken in by the most violent possible inspiration after the strongest possible expiration, that is, the supplemental, tidal, and complemental air together, is known as the *vital capacity.* For a healthy man

1.7 meters (5 feet 8 inches) high it is about 3,700 c. c. (225 cub. inches) and increases 60 c. c. for each additional centimeter of stature; or about 9 cub. inches for each inch of height. These figures are, of course, average figures. Individual variations from them are numerous.

The Quantity of Air Breathed Daily. Knowing the quantity of air taken in at each breath and expelled again (after more or less thorough admixture with the stationary air) we have only to know, in addition, the rate at which the breathing movements occur, to be able to calculate how much air passes through the lungs in twenty-four hours. The average number of respirations in a minute is found by counting on persons sitting quietly, and not knowing that their breathing rate is under observation, to be twelve to fifteen in a minute. In each respiration half a liter (30 cubic inches) of air is concerned; therefore 6 to 7.5 liters are breathed every minute, and 8,640 to 10,800 liters (300–375 cubic feet) in an ordinary day.

Types of Breathing. Since the diaphragm when it contracts pushes down the abdominal viscera beneath it, these have to make room for themselves by pushing out the soft front of the abdomen which, accordingly, protrudes when the diaphragm descends. Hence breathing mainly by the diaphragm, being indicated on the exterior by movements of the abdomen, is often called "abdominal respiration," as distinguished from breathing mainly by the ribs, called "costal" or "chest" breathing. The former type is more commonly seen, although if tight clothing is worn around the abdomen the latter type takes its place.

The Aspiration of the Thorax. As already pointed out, the external air cannot press directly upon the contents of the thoracic cavity, on account of the rigid framework which supports its walls; it still, however, presses on them indirectly through the lungs. Pushing on the interior of these with a pressure equal to that exerted on the same area by a column of mercury 760 mm. (30 inches) high, it distends them and forces them against the inside of the chest-walls, the heart, the great thoracic blood vessels, the thoracic duct, and the other contents of the chest cavity. The pressure against these organs is not equal to that of the external air, since some of the total air-pressure on the inside of the lungs is used up in overcoming their elasticity, and it is only

the residue which pushes them against the things outside them. In expiration this residue is equal to that exerted by a column of mercury 754 mm. (29.8 inches) high. On most parts of the Body the atmospheric pressure acts, however, with full force. Pressing on a limb it pushes the skin against the soft parts beneath, and these compress the blood- and lymph-vessels among them; and the yielding abdominal walls do not, like the rigid thoracic walls, carry the atmospheric pressure themselves, but transmit it to the contents of the cavity. It thus comes to pass that the blood and lymph in most parts of the Body are under a higher atmospheric pressure than they are exposed to in the chest, and consequently these liquids tend to flow into the thorax, until the extra distention of the vessels in which they there accumulate compensates for the less external pressure to which those vessels are exposed. An equilibrium would thus very soon be brought about were it not for the respiratory movements, in consequence of which the intrathoracic pressure is alternately increased and diminished, and the thorax comes to act as a sort of suction-pump on the contents of the vessels of the Body outside it; thus the respiratory movements influence the circulation of the blood and the flow of the lymph.

Influence of the Respiratory Movements upon the Circulation. Suppose the chest in a condition of normal expiration and the external pressure on the blood in the blood vessels within it and in the heart, to have come, in the manner pointed out in the last paragraph, into equilibrium with the atmospheric pressure exerted on the blood vessels of the neck and abdomen. If an inspiration now occurs, the chest cavity being enlarged the pressure on all of its contents will be diminished. In consequence, air enters the lungs from the windpipe, and blood enters the venæ cavæ and the right auricle of the heart from the outlying veins. When the next expiration occurs, and the pressure in the thorax again rises, air and blood both tend to be expelled from the cavity. Whatever extra blood has, to use the common phrase, been "sucked" into the intrathoracic venæ cavæ in inspiration and has not been sent already on into the right ventricle before expiration occurs, is, however, on account of the venous valves, prevented from flowing back whence it came, and is imprisoned in the cavæ under an increased pressure during expiration; and this tends to make

it flow faster into the auricle during the diastole of the latter. How much the alternating respiratory movements assist the venous flow is shown by the dilation of the veins of the head and neck which occurs when a person is holding his breath; and the blackness of the face, from distention of the veins and stagnation of the capillary flow, which occurs during a prolonged fit of coughing, which is a series of expiratory efforts without any inspirations.

The ventricles and arteries are not directly affected to any appreciable extent by the respiratory movements; their walls are too thick and the arterial pressure too great to respond to these small variations of intrathoracic pressure. The increase in venous flow which occurs during inspiration does, however, by supplying the heart with more blood at that time, bring about a small increase in arterial pressure during each inspiration. The increased blood-supply is handled by the heart through an augmentation of its beat. This has been shown to be brought about by an *irradiation* to the cardiac centers of the influences that govern the act of inspiration. To a marked extent the vigor of breathing and the heart-rate run parallel.

Influence of Breathing Movements on the Lymph-Flow. During inspiration, when intrathoracic pressure is lowered, lymph is pressed into the thoracic duct from the abdominal lymphatics. In expiration, when thoracic pressure rises again, the extra lymph cannot flow back on account of the valves in the lymphatic vessels, and it is consequently driven on to the cervical ending of the thoracic duct. The breathing movements thus pump the lymph on.

The Respiratory Center. The respiratory movements are to a certain extent under the control of the will; we can breathe faster or slower, shallower or more deeply, as we wish, and can also "hold the breath" for some time—but the voluntary control thus exerted is limited in extent; no one can commit suicide by holding his breath. In ordinary quiet breathing the movements are quite involuntary; they go on perfectly without the least attention on our part, and not only in sleep, but during the unconsciousness of fainting or of an apoplectic fit. The natural breathing movements are therefore either reflex or automatic.

The muscles concerned in producing the changes in the chest which lead to the entry or exit of air are of the ordinary skeletal

type; and these, as we have seen, only contract in the Body under the influence of the nerves going to them; the nerves of the diaphragm are the two phrenic nerves, one for each side of it; the external intercostal muscles are supplied by certain branches of the thoracic spinal nerves, called the intercostal nerves. If the phrenic nerves be cut the diaphragm ceases its contractions, and a similar paralysis of the external intercostals follows section of the intercostal nerves.

Since the inspiratory muscles only act when stimulated by nervous impulses reaching them, we have next to seek where these impulses originate; and experiment shows that it is in the *medulla oblongata*. All the brain of a cat or a rabbit in front of the medulla can be removed, and it will still go on breathing; and children are sometimes born with the medulla only, the rest of the brain being undeveloped, and yet they breathe for a time. If, on the other hand, the spinal cord be divided immediately below the medulla of an animal, all breathing movements of the chest cease at once. We conclude, therefore, that the nervous impulses calling forth contractions of the respiratory muscles arise in the medulla, and travel down the spinal cord and thence out along the phrenic and intercostal nerves. This is confirmed by the fact that if the spinal cord be cut across below the origin of the fourth pair of cervical spinal nerves (from which the phrenics mainly arise) but above the first thoracic spinal nerves, the respiratory movements of the diaphragm continue, but those of the intercostal muscles cease; this phenomenon has sometimes been observed on men so stabbed in the back as to divide the spinal cord in the region indicated. Finally, that the nervous impulses exciting the inspiratory muscles originate in the medulla, is proved by the fact that if a small portion of that organ, the so-called *vital knot*, be destroyed, all the respiratory movements cease at once and forever, although all the rest of the brain and spinal cord may be left uninjured. This part of the medulla is known as the *respiratory center*.

Is the Respiratory Center Reflex? Since this center goes on working independently of the will, we have next to inquire, Is it a reflex center or not? Are the efferent discharges it sends along the respiratory nerves due to afferent impulses reaching it by centripetal nerve-fibers? Or does it originate efferent nervous impulses independently of excitation through afferent nerves?

We know, in the first place, that the respiratory center is largely under reflex control; a dash of cold water on the skin, the irritation of the nasal mucous membrane by snuff, or of the larynx by a foreign body, will each cause a modification in the respiratory movements—a long indrawn breath, a sneeze, or a cough. But, although thus very subject to influences reaching it by afferent nerves, the respiratory center seems essentially independent of such. In many animals, as rabbits (and in some men), marked breathing movements take place in the nostrils, which dilate during inspiration; and when the spinal cord of a rabbit is cut close to the medulla, and the chief sensory cranial nerves are also divided, so as to cut off the respiratory center from almost all possible afferent nervous impulses, regular breathing movements of the nostrils continue, even though the respiratory movements proper have ceased, through cutting off the connection of the breathing muscles with the respiratory center. We conclude, therefore, that the activity of the respiratory center, however much it may be capable of modification through sensory nerves, is essentially independent of them.

What it is that Excites the Respiratory Center. It has long been recognized that the activity of the respiratory center is related to the condition of the blood flowing through it; arterial blood excites it feebly or not at all; venous blood excites it powerfully, and more and more strongly as its venosity increases. The difference between arterial and venous blood is primarily a difference in the relative amounts of oxygen and of carbon dioxid present therein. The question is: Does venous blood owe its ability to stimulate the respiratory center to its low oxygen content or to its high content of carbon dioxid? Experiment has shown that both factors enter somewhat, but that the center is more affected by small changes in the amount of carbon dioxid than by small changes in the amount of oxygen.

We might look upon carbon dioxid as the main regulator of the respiratory center, and for convenience of description shall do so. As a matter of exactness, however, not carbon dioxid as such but an acid condition of the center, dependent chiefly on carbon dioxid, determines its activity. Lack of oxygen may produce indirectly the same acid condition that is brought about by excess of carbon dioxid. We picture the center as consisting of a group of nerve-

cells in which metabolic processes go on, even during rest (basic metabolism), giving rise to acids. If oxygen is present in sufficient quantity the acid formed is carbonic, H_2CO_3 *i. e.*, CO_2+H_2O; when oxygen is deficient lactic or some similar acid will accumulate instead; the metabolic processes are assumed to be in the main similar to those previously described as going on in muscle (p. 112). The center is supposed to be excited by some definite degree of acidity, not necessarily the same in all persons, nor in the same person at all times. Whenever its acidity is below this critical level the center remains quiescent; whenever it rises above the same the center discharges, and more vigorously the more acid it becomes.

Discharges from the Center Act to Correct its Overacidity. The automatic control of breathing depends on the fact stated in the paragraph heading, *i. e.*, that the more acid the center becomes the more do its discharges tend to overcome its acidity. Several steps are involved; these must be grasped in relation one to another in order for the process as a whole to be clear. In the first place we have the fact that the acidity of the center can be reduced in only one way, namely, by diffusion of the acid out into the blood; since the acids are either carbonic or (presumably) lactic, outward diffusion depends on there being a less concentration of these particular acids in the blood than in the center; diffusion taking place only when a difference in concentration exists. In the blood (but apparently not in the respiratory center) both acids combine for the most part with sodium salts to form sodium bicarbonate and sodium lactate respectively (see next chapter). For reasons to be brought out later this does not, however, greatly affect the diffusion process as a whole, so that excess of bicarbonate or lactate in the blood interferes with the escape of the corresponding acids from the center about as much as the acids themselves would. We have to bear in mind at this point that the respiratory center is not alone in pouring acids out into the blood; all the tissues are doing the same, and such as are active at a very rapid rate.

We can start with an imagined situation in which the acidity of the respiratory center is below the critical level, hence it is not discharging and no breathing movements are being made. The blood is receiving carbon dioxid from all the tissues and supplying them with oxygen if it happens to have any in it at the moment selected for starting the description; if the blood is short of oxygen

the tissues will not receive the amounts necessary to enable them to perform recovery oxidations (p. 116) and lactates will be poured out into the blood instead of carbon dioxid. As the blood flows through the capillaries of the lung alveoli carbon dioxid will diffuse out to the alveolar air and oxygen into the blood from the same; but since no positive lung ventilation is going on these processes will gradually fall off, due to the depletion of the alveolar air in respect to oxygen and its rising concentration of carbon dioxid. As the interchanges between alveolar air and blood decline the latter becomes more and more deficient in oxygen and more and more charged with bicarbonates and lactates; thus the diffusion outward of acids from the respiratory center to the blood is interfered with and the center becomes more and more acid. In course of time the acidity passes the critical level and the center begins to discharge nerve impulses to the muscles of inspiration. The resulting breathing movement causes atmospheric air to enter the alveoli, raising the oxygen concentration of the air in the same and lowering the carbon dioxid concentration; thus renewed interchanges with blood become possible, and hence, in turn, renewed escape of acids from the respiratory center.

Why are the Respiratory Discharges Rhythmic? If a certain level of acidity is the stimulus for the respiratory center, why does that center act rhythmically? Does the carbon dioxid (bicarbonate) content of the circulating blood increase and decrease twelve or more times a minute sufficiently to excite and cease to excite the center at that rhythm? The answer to this question is afforded by a simple experiment. If in an animal breathing naturally under anesthesia both vagus nerves are cut there is an immediate change in the character of the respirations. From being rapid and shallow they become very deep and take on a much slower rate. Under this condition we may properly assume that the respirations do follow the carbon dioxid content of the blood; the center begins to discharge when the blood contains enough carbon dioxid so that its acidity rises above the critical level, and continues its discharge until the aëration of the blood, resulting from the inspiration, lowers the carbon dioxid below the point of stimulation. There follows a period of expiration and rest which continues until sufficient carbon dioxid has again accumulated to start the action anew.

Since with the vagus nerves cut the respirations follow the carbon dioxid concentration of the blood, but with the nerves intact do not, being much more shallow and rapid, we must determine the influence of the vagus nerves upon the center in order to understand ordinary breathing. It has been shown that the influence of the vagus nerves is a simple reflex one. These nerves contain sensory fibers arising in the lung tissue and so situated as to be stimulated mechanically every time the lung is inflated. The impulses conveyed over these fibers to the central nervous system are inhibitory to the respiratory center. Bearing this action of the vagus fibers in mind we may account for normal breathing thus; the blood contains enough carbon dioxid all the time, under ordinary circumstances, to keep the acidity of the respiratory center above the critical level of excitation; whenever the center discharges under this stimulus it brings about movements of inspiration which result in expansion of the lungs; whenever the lungs expand the sensory fibers contained in their walls are stimulated and so inhibitory influences are sent to the respiratory center. Inspiration proceeds, then, until the inhibitory impulses from the lungs overcome the stimulus of acidity, when it comes to an end and the thorax falls back to the position of rest. This falling back, which constitutes normal expiration, collapses the lungs somewhat; the inhibitory impulses diminish or disappear; and the stimulating action due to the acidity again becomes effective. Thus in normal breathing inspiration and expiration follow one another without any pause between, and the respirations are shallow because the inhibition cuts them off almost as soon as started.

The entire significance of breathing is to ventilate the lungs. It is relatively a minor matter whether a system of rapid shallow breaths or of slow deep ones is used so long as the result is secured. The necessary amount of air would be taken into and discharged from the lungs every minute by either arrangement. There is probably some advantage to the Body in the rapid shallow type in avoiding such wide fluctuations in the concentrations of the respiratory gases in the blood and the alveoli as would occur with slower and deeper breathing.

Forced Expiration. Although in ordinary quiet breathing, as we have seen, expiration is a passive collapse of the chest, active expiratory effort is of frequent occurrence. In talking, singing,

whistling, as well as in coughing, sneezing, and straining, the expiratory muscles are functioning. The ease with which these are brought into play suggests that the part of the center which controls them, although not normally in action, is hung on a "hair trigger" so to speak, requiring very slight additional influence to arouse it to action.

Sensitiveness of the Respiratory Center. The respiratory center is responsive to very slight changes in the amount of carbon dioxid in the blood. A small increase quickens the breathing notably. The effect of the quickened breathing is to ventilate the lungs more thoroughly, and thus to bring about a more rapid movement of carbon dioxid from the blood to the alveolar air (see next chapter). In this manner the increased amount of carbon dioxid is got rid of. The respiratory center may be thought of as a delicate governor which serves to keep the carbon dioxid content of the blood at a uniform level. The chief source of carbon dioxid is in the active muscles. Muscular exercise is, therefore, the most common cause of quickened breathing. Incidentally the changes in lung ventilation which serve to keep the carbon dioxid level steady have the effect at the same time of regulating the supply of available oxygen. Thus an increase in carbon dioxid brings about a more pronounced ventilation of the lungs, and thus, in turn provides more oxygen than is brought to the lungs during ordinary breathing. There will be no need for a change in the amount of oxygen unless there is a change in the bodily oxidations, so whenever more oxygen is needed the need is signalized by an increase in the carbon dioxid, and this acts to bring into play the mechanism by which the required oxygen is supplied.

Eupnea, Hyperpnea, Dyspnea, Apnea. Ordinary quiet breathing is known as *eupnea*. Rapid breathing, such as follows moderate exercise, is designated as *hyperpnea*. When the breathing is forced, and especially when forced expiration enters, we have the condition called *dyspnea*. This results from abnormal excitement of the respiratory center either reflexly, as from stimulation of pain nerves, or by a greater increase in the carbon dioxid content of the blood than that which causes simple hyperpnea. The dyspnea of the early stages of suffocation arises from this latter cause. *Apnea*, or absence of breathing, may result from one of two conditions or from both acting together. The first

of these is a lowering of the concentration of carbon dioxid in the blood as by voluntary overbreathing, so that the respiratory center is not stimulated. The second is inhibition of the center through vigorous and repeated inflation of the lungs. Since inflation of the lungs with ordinary air brings about both conditions the apnea which results from this treatment is partly chemical and partly inhibitory. That inhibition enters in the production of apnea in this way is shown by the greater difficulty of producing the condition in animals with both vagi cut.

Holding the Breath. When one holds his breath he is sending volitional impulses to the respiratory center which inhibit its discharge. Meanwhile the bodily oxidations go right on, so the longer this inhibition continues the greater becomes the amount of carbon dioxid in the blood, and the higher does the acidity of the center rise. In a very short time the acid stimulation becomes more potent than the volitional inhibition, and when that time comes a breath must be taken in spite of the effort to hold it. Evidently any procedure that will diminish the amount of carbon dioxid in the blood to begin with will prolong the time the breath can be held. This can be done by forced breathing for several minutes. The overventilation of the lungs thus carried on sweeps out so much carbon dioxid from the blood that a much longer time elapses than ordinarily before the accumulation overcomes the volitional inhibition. Since, as we shall learn (p. 444), overventilation of the lungs does not materially increase the supply of available oxygen, this procedure may bring about severe oxygen deficiency, which shows itself by blueness of the skin and mucous membranes, a blueness caused by the excessively venous condition of the blood in the capillaries and small veins.

Asphyxia. Asphyxia is suffocation, or the combination of excessive accumulation of carbon dioxid with want of oxygen by the tissues. It may be brought about in various ways; as by strangulation, which prevents the entry of air into the lungs; or by breathing an atmosphere containing five or six per cent of carbon dioxid. The symptoms, described in the next paragraph, are due to the accumulation of acid, first in the respiratory center and secondarily, when violent convulsions occur, in other parts of the central nervous system as well. Lack of oxygen plays its part only in bringing about excess production of lactic acid,

which seems to be more potent than carbonic as a stimulus to the center.

The Phenomena of Asphyxia. As the bicarbonates and lactates in the blood rise above the normal amount the breathing becomes hurried and deeper, and the accessory muscles of respiration are called into activity. The dyspnea becomes more and more marked, and this is especially the case with the expirations which, almost or quite passively performed in natural breathing, become violently muscular. At last nearly all the muscles in the Body are set at work; the rhythmic character of the respiratory acts is lost, and general convulsions occur, but, on the whole, the contractions of the expiratory muscles are more violent than those of the inspiratory.

The violent excitation of the nerve-centers soon exhausts them, and all the more readily since their oxygen supply (which they like all other tissues need in order to continue their activity) is cut off. The convulsions therefore gradually cease, and the animal becomes calm again, save for an occasional act of breathing: these final movements are inspirations and, becoming less and less frequent, at last cease, and the animal appears dead. Its heart, however, though gorged with extremely dark venous blood, still makes some slow feeble pulsations. So long as it beats artificial respiration can restore the animal, but once the heart has finally stopped restoration is impossible. There are thus three distinguishable stages in death from asphyxia. (1) The stage of dyspnea. (2) The stage of convulsions. (3) The stage of exhaustion; the convulsions having ceased but there being from time to time an inspiration. The end of the third stage occurs in a mammal about five minutes after the oxygen supply has been totally cut off. If the asphyxia be due to a partial, and not a complete, strangulation, of course all the stages take longer.

Artificial Respiration. Asphyxia from drowning and other causes occurs with lamentable frequency these days, and there is no doubt that many lives are sacrificed through ignorance on the part of bystanders of the proper restorative procedures. There are several methods of applying artificial respiration to human beings. The method of Schaefer is as effective as any. The following description is quoted from his paper on the subject: "The method consists in laying the subject in the prone posture, preferably on

the ground, with a thick folded garment underneath the chest and epigastrium (upper part of abdomen). The operator puts himself athwart or at the side of the subject, facing his head and places his hands on each side over the lower part of the back (lowest ribs). He then slowly throws the weight of his Body forward to bear upon his own arms, and thus presses upon the thorax of the subject and forces air out of the lungs. This being effected, he gradually relaxes the pressure by bringing his own Body up again to a more erect position, but without moving the hands." These movements should be repeated about fifteen times a minute until normal breathing is resumed, and should not be given up for at least a half hour if recovery does not occur sooner. If there is water in the lungs it should be allowed to drain out before the artificial respiration is begun. Otherwise it may be churned into a foam by the movements, and defeat the desired ventilation of the lungs.

Anoxemia. This is a condition in which there is no interference with the escape of carbon dioxid from the blood, but the oxygen supply is seriously reduced or cut off altogether. It is most commonly brought on by ascending to high altitudes where the diminution in atmospheric pressure includes an equivalent diminution in the oxygen supply. Anoxemia may be induced experimentally by exposure in an atmosphere containing no oxygen; or by putting an animal in a vacuum; or by making it breathe air containing a gas which has a stronger affinity for hemoglobin than oxygen has, and which, therefore, turns the oxygen out of the red corpuscles and takes its place. The gases which do the latter are very interesting since they serve to prove conclusively that the Body can live only by the oxygen carried around by the hemoglobin of the red corpuscles; the amount dissolved in the blood-plasma being insufficient for its needs. Of such gases carbon monoxid is the most important and best studied; in the frequent mode of committing suicide by stopping up all the ventilation holes of a room and turning on the gas, it is poisoning by carbon monoxid which causes death.

Anoxemia is of practical importance to aviators and mountain climbers; to the latter particularly, because they cannot have ready supplies of oxygen along in tanks as aviators can, except at sacrifice of strength which is urgently needed for the labor of climbing itself. At altitudes of 14,000 feet or over

most unacclimatized persons develop symptoms due to anoxemia. These range from a slight dulling of the senses to severe depression, gastero-intestinal disturbances, and in severe cases convulsive seizures or even partial paralysis. Of course death inevitably results from extreme anoxemia. An interesting early symptom of marked anoxemia is a "fixation of ideas"; the individual cannot shift his attention from the position it has when the anoxemia comes on. This is a source of danger to aviators, who require to be mentally alert at all times, and never more than when at very high altitudes. The obvious precaution is to require breathing of oxygen from tanks to begin when dangerous altitudes are approached, regardless of the subjective feelings of the aviator.

Acclimatization. Persons who live at high altitudes suffer much less than most casual visitors do. This is because they become *acclimatized*. The bodily changes are two; there is first a marked increase in the number of red corpuscles, which may be so great as to amount to a fifty per cent augmentation of the quantity of hemoglobin available for carrying oxygen; the second change is in the composition of the red corpuscles as a whole, so that the hemoglobin they contain is more efficient than before in carrying oxygen. Thus in spite of the diminution in oxygen pressure the blood carries what is available so much more effectively as to make up the difference.

Modified Respiratory Movements. *Sighing* is a deep, long-drawn inspiration followed by a shorter but correspondingly large expiration. *Yawning* is similar, but the air is mainly taken in by the mouth instead of the nose, and the lower jaw is drawn down in a characteristic manner. *Hiccough* depends upon a sudden contraction of the diaphragm, while the aperture of the larynx closes; the entering air, drawn through the narrowing opening, causes the peculiar sound. *Coughing* consists of a full inspiration followed by a violent and rapid expiration, during the first part of which the laryngeal opening is kept closed; being afterwards suddenly opened, the air issues forth with a rush, tending to carry out with it anything lodged in the windpipe or larynx. *Sneezing* is much like coughing, except that, while in a cough the isthmus of the fauces is held open and the air mainly passes out through the mouth, in sneezing the fauces are closed and the blast is driven through

the nostrils. It is commonly excited by irritation of the nasal mucous membrane, but in many persons a sudden bright light falling into the eye will produce a sneeze. *Laughing* consists of a series of short expirations following a single inspiration; the larynx is open all the time, and the vocal cords (Chap. XXXIII) are set in vibration. *Crying* is, physiologically, much like laughing and, as we all know, one often passes into the other. The accompanying contractions of the face muscles giving expression to the countenance are, however, different in the two.

All these modified respiratory acts are essentially reflex and they serve to show to what a great extent the discharges of the respiratory center can be modified by afferent nerve impulse; but, with the exception of hiccough, they are to a certain extent, like natural breathing, under the control of the will. Most of them, too, can be imitated more or less perfectly by voluntary muscular movements; though a good stage sneeze or cough is rare.

CHAPTER XXIV

RESPIRATION. THE GASEOUS INTERCHANGES

Nature of the Problems. The study of the respiratory process from a chemical standpoint has for its object to discover what are, in kind and extent, the gaseous interchanges between the air in the lungs and the blood in the pulmonary capillaries; and the nature and amount of the corresponding changes between the living tissues, and the blood in the systemic capillaries. Neglecting for the time the oxygen used up in forming water, and some carbon dioxid eliminated by other organs than the lungs, these processes in the long run balance, the blood losing as much carbon dioxid gas in the lungs as it gains elsewhere, and gaining as much oxygen in the lungs as it loses in the systemic capillaries. To comprehend the matter it is necessary to know the physical and chemical conditions of these gases in the lungs, in the blood, and in the tissues generally; for only so can we understand how it is that in different localities of the Body such exactly contrary processes occur.

The Changes Produced in Air by Being Once Breathed. These are fourfold—changes in its temperature, in its moisture, in its chemical composition, and its volume.

The air taken into the lungs is nearly always cooler than that expired, which has a temperature of about 36° C. (97° F.). The temperature of a room is usually not far from 21° C. (70° F.). The warmer the inspired air the less, of course, the heat which is lost to the Body in the breathing process; its average amount is calculated as about equal to 50 Calories in twenty-four hours; a Calorie being as much heat as will raise the temperature of one kilogram (2.2 lbs.) of water one degree centigrade (1.8° F.).

The inspired air always contains more or less water vapor, but is rarely saturated; that is, rarely contains so much but it can take up more without showing it as mist; the warmer air is, the more water vapor is required to saturate it. The expired air is nearly saturated for the temperature at which it leaves the Body, as is readily shown by the water deposited when it is slightly

cooled, as when a mirror is breathed upon; or by the clouds seen issuing from the nostrils on a frosty day, these being due to the fact that the air, as soon as it is cooled, cannot hold all the water vapor which it took up when warmed in the Body. Air, therefore, when breathed once, gains water vapor and carries it off from the lungs; the actual amount being subject to variation with the temperature and saturation of the inspired air: the cooler and drier that is, the more water will it gain when breathed. On an average the amount thus carried off in twenty-four hours is about 255 grams (9 ounces). To evaporate this water in the lungs an amount of heat is required, which disappears for this purpose in the Body, to reappear again outside it when the water vapor condenses. The amount of heat taken off in this way during the day is about 148 Calories. The total daily loss of heat from the Body through the lungs averages therefore 198 Calories, 50 in warming the inspired air and 148 in the evaporation of water.

The most important changes brought about in the breathed air are those in its chemical composition. Pure air when completely dried consists in each 100 parts of:

	By Volume	By Weight
Oxygen	21	23
Nitrogen	79	77

Ordinary atmospheric air contains in addition 4 volumes of carbon dioxid in 10,000, or 0.04 in 100, a quantity which, for practical purposes, may be neglected. When breathed once, such air gains rather more than 4 volumes in 100 of carbon dioxid, and loses a little less than 5 of oxygen. More accurately, 100 volumes of expired air after drying contain:

Oxygen	16.6
Nitrogen	79.
Carbon dioxid	4.4

Since 8,640 liters (300 cubic feet) of air are breathed in twenty-four hours and lose 5 per cent of oxygen, the total quantity of this gas taken up in the lungs daily is $8{,}640 \times 5 \div 100 = 432$ liters (of course an average figure, subject to wide variations from individual to individual and from day to day). One liter of oxygen measured at 0° C. (32° F.) and under a pressure equal to one

atmosphere, weighs 1.43 grams, so the total weight of oxygen taken up by the lungs daily is $432 \times 1.43 = 627$ grams (22 ounces).

The amount of carbon dioxid excreted from the lungs being 4.4 per cent of the volume of the air breathed daily, is $8{,}640 \times 4.4 \div 100 = 380$ liters measured at the normal temperature and pressure. This volume weighs 744 grams, or 26 ounces. If all the oxygen taken in were breathed out again as carbon dioxid the volume of the latter should equal that of the oxygen breathed in. The discrepancy results from the fact that not all the oxygen combines with carbon; some of it unites with hydrogen to form water. The water thus formed simply adds itself to the general water content of the Body, and has no bearing on the amount discharged in the expired air; this latter depending, as already stated, on the rate of evaporation from the lung surface.

If the expired air be measured as it leaves the Body its bulk will be found greater than that of the inspired air, since it not only has water vapor added to it, but is expanded in consequence of its higher temperature. If, however, it be dried and reduced to the same temperature as the inspired air its volume will be found diminished, since it has lost 5 volumes per cent of oxygen and gained only 4.4 of carbon dioxid. In round numbers, 100 volumes of dry inspired air at zero, give 99 volumes of dry expired air measured at the same temperature and pressure.

Ventilation. Since at every breath some oxygen is taken from the air and some carbon dioxid given to it, were the atmosphere around a living man not renewed he would obviously die, in course of time, of asphyxiation. The fact is, however, that air becomes unfit to breathe long before the depletion of oxygen and accumulation of carbon dioxid reach a stage even remotely approaching that of asphyxiation. For many years this was thought to be due to the exhalation of organic poisons from the lungs, but recent careful studies have thrown grave doubt on the presence of even minute traces of such poisons, and have shown for a certainty that none are formed and exhaled in amounts sufficient to account for the bad effects of close air. It is true that ill-smelling effluvia are given off from the Body, chiefly from the sweat-glands and alimentary tract, and these contribute greatly to the disagreeable character of close air, but the actual ill effects seen in persons who

stay too long in ill-ventilated rooms are now known to be due to the excessive heat and moisture present in them.

The Body gives off both heat and water vapor continuously. If a number of persons are in the same room, and the air in it is not changed, the relative humidity rises rapidly, as does also the temperature. Continued breathing of this over-moist and over-warm air causes the familiar symptoms of discomfort, depression, and often headache which we associate with bad ventilation. Modern ventilation engineering, as applied to schools, churches, and large office buildings, recognizes the fact that air is only very gradually exhausted of its oxygen to a serious degree, or unduly impregnated with carbon dioxid. Accordingly these are not specifically looked out for in planning ventilation systems. The measures taken are for the purpose of preventing moisture from accumulating to excess, of keeping the temperature down to a comfortable level, and of removing malodorous substances from the atmosphere. The method used is that of circulating the same air over and over again, washing it at some point in the circuit to remove odorous gases, and incidentally dust particles, then withdrawing excess moisture, and finally either warming or cooling the air to the desired temperature. The air is circulated at a rate such that each person is supplied about 15 cubic feet per minute. Since there is always some loss to the exterior through fireplace flues, open doors, etc., a small current of fresh outside air is pumped in more or less continuously; this suffices to make good the oxygen depletion, just as the incidental losses take care of the accumulating carbon dioxid.

In the ventilation of homes and small detached schoolrooms elaborate installations of the kind indicated above are, of course, out of the question. The alternative is to keep the room air reasonably fresh, *i. e.*, like outside air. Ventilation does not necessarily imply draughts of cold air, as is often supposed. In warming by indirect radiation (the ordinary hot-air furnace) it may readily be secured by arranging, in addition to the registers from which the warmed air reaches the room, proper openings at the opposite side, by which the old air may pass off to make room for the fresh. An open fire in a room will always keep up a current of air through it, and is the healthiest, though not the most economical, method of warming an apartment.

In severe weather, when there is a tendency to keep rooms rather tightly closed, a good plan is to open widely all doors and windows for a few minutes each day, allowing fresh air to penetrate to every corner, sweeping out the old air before it. This daily renewing, helped out by such ventilation as is afforded by ill-fitting doors and windows, usually keeps the air of rooms in respirable condition when not occupied by too many persons. The modern habit of sleeping summer and winter in rooms with open windows is to be highly commended, and should be even more generally adopted. In fact the more outdoor air one can have, and at the same time keep warm, the better for the bodily well-being. The beneficial effects of fresh air and sunshine, especially for children and in pulmonary tuberculosis, cannot be too strongly emphasized.

An important fact in ventilation, bearing on *bodily comfort*, is that too low humidity is to be avoided as well as too high. An ordinary fault in ventilation is that the air is allowed to become too dry. This is particularly true during the winter months when artificial heat is used. To maintain the desired humidity in dwelling houses of ordinary size during cold weather from $1^1/_2$ to 2 gallons of water should be evaporated in the house daily. Where large numbers of house plants are kept the evaporation from their leaves will contribute materially toward this amount.

Changes undergone by the Blood in the Lungs. These are the exact reverse of those undergone by the breathed air—what the air gains the blood loses, and *vice versa*. Consequently, the blood loses heat, and water, and carbon dioxid in the pulmonary capillaries; and gains oxygen. These gains and losses are accompanied by a change of color from the dark purple which the blood exhibits in the pulmonary artery, to the bright scarlet it possesses in the pulmonary veins.

The dependence of this color change upon the access of fresh air to the lungs while the blood is flowing through them, can be readily demonstrated. If a rabbit be rendered unconscious by chloroform, and its chest be opened, after a pair of bellows has been connected with its windpipe, it is seen that, so long as the bellows are worked to keep up artificial respiration, the blood in the right side of the heart (as seen through the thin auricle) and that in the pulmonary artery, is dark colored, while that in the pulmonary veins and the left auricle is bright red. Let, however,

the artificial respiration be stopped for a few seconds and, consequently, the renewal of the air in the lungs (since an animal cannot breathe for itself when its chest is opened), and very soon the blood returns to the left auricle as dark as it left the right. In a very short time symptoms of suffocation show themselves and the animal dies, unless the bellows be again set at work.

In a former paragraph (p. 435) we saw that about 5 volumes in 100 of oxygen are absorbed from the alveolar air into the blood, and 4.4 in 100 of carbon dioxid given off to the alveolar air from the blood. If we put the amount of air inhaled and exhaled with each breath (tidal air) at 500 c. c. and the respiratory rate at 12 per minute, we have 6,000 c. c. of air involved each minute, 5 per cent of this, or 300 c. c., would give the oxygen consumption and 4.4 per cent, or 264 c. c., the carbon dioxid output in the same time. Direct determinations of the oxygen absorption and the carbon dioxid output of persons at rest ordinarily give about 280–325 c. c. per minute for oxygen and 250-280 c.c. for carbon dioxid, figures agreeing fairly well with those calculated from the volume of air breathed.

The Blood Gases. If fresh blood be rapidly exposed to as complete a vacuum as can be obtained, it gives off certain gases, known as the *gases of the blood.* These are the same in kind, but differ in proportion, in venous and arterial blood; there being more carbon dioxid and less oxygen obtainable from the venous blood going to the lungs by the pulmonary artery, than from the arterial blood coming back to the heart by the pulmonary veins. The gases given off by venous and arterial blood, measured under the normal pressure and at the normal temperature, amount to from 68 to 70 volumes for every 100 volumes of blood, and in the two cases are about as follows:

	Venous Blood	Arterial Blood
Oxygen	14.5	19.5
Carbon dioxid	54.4	50
Nitrogen	1.7	1.7

It is important to bear in mind that while arterial blood contains some carbon dioxid that can be removed by the air-pump, venous blood also contains some oxygen removable in the same way; so that the difference between the two is only one of degree. When an animal is killed by suffocation, however, the last trace of

oxygen which can be yielded up in a vacuum disappears from the blood before the heart ceases to beat. All the blood of such an animal is what might be called asphyxial blood, and has a far darker color than ordinary venous blood.

The Cause of the Bright Color of Arterial Blood. The color of the blood depends on its red corpuscles, since pure blood-plasma or blood-serum is colorless, or at most a very faint straw yellow. Hence the color change which the blood experiences in circulating through the lungs must be due to some change in its red corpuscles. We have already seen (Chap. XVII) that the functional substance of the red corpuscles is *hemoglobin*, which has the property of combining with oxygen. Hemoglobin itself is of a dark purplish color, when combined with oxygen the resulting compound is a bright scarlet. Hemoglobin combined with oxygen is known as *oxyhemoglobin*, and it is on its predominance that the color of arterial blood depends. Hemoglobin uncombined with oxygen, named *reduced hemoglobin*, predominates in venous blood, and is the only kind found in the blood of a suffocated mammal.

The Laws Governing the Absorption of Gases by a Liquid. In order to understand the condition of the gases in the blood liquid it is necessary to recall the general laws in accordance with which liquids absorb gases. They are as follows:

1. A given volume of a liquid at a definite temperature absorbs any gas to which it is exposed, and if it does not combine chemically with it, takes up an amount of the gas which depends upon two things: (1) the solubility of the gas in the liquid; and (2) the pressure of the gas upon the surface of the liquid. As the pressure of the gas is increased the amount of it which goes in solution in the liquid is increased in exactly the same proportion. If a complete vacuum be formed above a liquid all the gas contained within it is given off. This law, that the quantity of a gas dissolved by a liquid varies directly as the pressure of that gas on the surface of the liquid is known as Henry's law.

Gas thus held in a liquid by pressure of the same gas overlying it is under a *tension* which depends on the pressure of the overlying gas and is considered to be numerically equal to it. That is, a gas dissolved in a liquid under an overlying pressure of one atmosphere is said to be under one atmosphere tension in the solution.

2. The amount of a gas dissolved by a liquid depends, not on

the total pressure exerted by all the gases pressing on its surface, but on the fraction of the total pressure which is exerted by the particular gas in question. For example, the average atmospheric pressure is equal to that of a column of mercury 760 mm. (30 inches) high. But 100 volumes of air contain approximately 80 volumes of nitrogen and 20 of oxygen; therefore about $\frac{1}{5}$ of the total pressure is due to oxygen and $\frac{4}{5}$ to nitrogen: and the amount of oxygen absorbed by water is just the same as if all the nitrogen were removed from the air and its total pressure therefore reduced to $\frac{1}{5}$ of 760 mm. (30 inches) of mercury; that is, to 152 mm. (6 inches) of mercury pressure. It is only the fraction of the total pressure exerted by the oxygen itself which affects the quantity of oxygen absorbed by water at any given temperature. So, too, of all the atmospheric pressure $\frac{4}{5}$ is due to nitrogen, and all the oxygen might be removed from the air without affecting the quantity of nitrogen which would be absorbed from it by a given volume of water. The atmospheric pressure would then be $\frac{4}{5}$ of 760 mm. of mercury, or 608 mm. (24 inches), but it would all be due to nitrogen gas—and be exactly equal to the fraction of the total pressure due to that gas before the oxygen was removed from the air. When several gases are mixed together the fraction of the total pressure exerted by each one is known as the *partial pressure* of that gas; and it is this partial pressure which determines the amount of each individual gas dissolved by a liquid. If a liquid exposed to the air for some time had taken up all the oxygen and nitrogen it could at the partial pressures of those gases in the air, and were then put in an atmosphere in which the oxygen had all been replaced by nitrogen, it would now give off all its oxygen, since, although the total gaseous pressure on it was the same, no part of it was any longer due to oxygen; and at the same time it would take up one-fifth more nitrogen, since the whole gaseous pressure on its surface was now due to that gas, while before only four-fifths of the total was exerted by it. If on the contrary, the liquid were exposed to pure hydrogen under a pressure of one atmosphere it would give off all its previously dissolved oxygen and nitrogen, since none of the pressure on its surface would now be due to those gases; and would take up as much hydrogen as corresponded to a pressure of that gas equal to 760 mm. of mercury (30 inches).

3. The amount of gas taken up by a liquid varies, other things being equal, *inversely* as the temperature.

4. Substances are known which combine chemically with certain gases in proportion to their tensions in solution. The hemoglobin of the blood is such a substance, and it combines with oxygen to form oxyhemoglobin in accordance with this law. In effect the situation is this: when a hemoglobin solution is exposed to an atmosphere containing only a small percentage of oxygen, and in which, accordingly, the partial pressure of the gas is low, only a small proportion of the hemoglobin molecules enter into combination with oxygen. If the percentage of oxygen in the atmosphere is increased, raising the tension of the gas in solution to correspond, a larger and larger proportion of the hemoglobin molecules enter into combination with it, until at some definite oxygen tension all the hemoglobin molecules become thus converted into oxyhemoglobin, at which point we speak of the hemoglobin, as being *saturated* with oxygen. Obviously if a hemoglobin-oxyhemoglobin mixture, which has been obtained by exposing hemoglobin to an oxygen-containing atmosphere, is removed to another atmosphere in which the oxygen-pressure is less than in the first, some of the oxyhemoglobin molecules will give off their oxygen until the proportion characteristic of the oxygen-pressure of the new atmosphere is reached; if placed in an oxygen-vacuum all the oxyhemoglobin will decompose, leaving only hemoglobin.

5. A membrane, moistened by a liquid in which a gas is soluble, does not essentially alter the laws of absorption, by a liquid on one side of it of a gas present on its other side, whether the absorption be due to mere solution or to chemical combinations or to both.

The Absorption of Oxygen by the Blood. Applying the physical and chemical facts stated in the preceding paragraph to the blood, we find that the blood contains (1) plasma, which simply dissolves oxygen, and (2) *hemoglobin*, which combines with it in proportion to its tension in the plasma.

Blood-plasma or, what comes to the same thing, fresh serum, exposed to the air, takes up a little less oxygen than so much water: about 0.25 volume of the gas for every 100 of the liquid, at Body temperature. This quantity obeys Henry's law.

If fresh defibrinated blood be employed, the quantity of oxygen taken up is much greater; this extra quantity is taken up by the

hemoglobin of the red corpuscles and it does not obey Henry's law. Instead it obeys the law of combination in proportion to tension, as outlined in (4) above. The actual quantity (in arterial blood) depends on the pressure of oxygen in the air in the alveoli of the lungs. This, in turn, depends on the efficiency with which the lungs are ventilated (p. 425). The adjustment, although dependent, as we saw in the last chapter, on the condition of acidity in the cells of the respiratory center, and not directly on the oxygen supply, works out so that under almost all situations of rest or bodily activity the partial pressure of oxygen in the alveolar air is about two-thirds that of ordinary atmospheric air (100 mm. Hg., as compared with 152 mm. Hg. in ordinary air).

Hemoglobin of Arterial Blood Nearly Saturated. To determine the extent to which hemoglobin combines with oxygen at any given tension reference may be made to figure 127, which is a

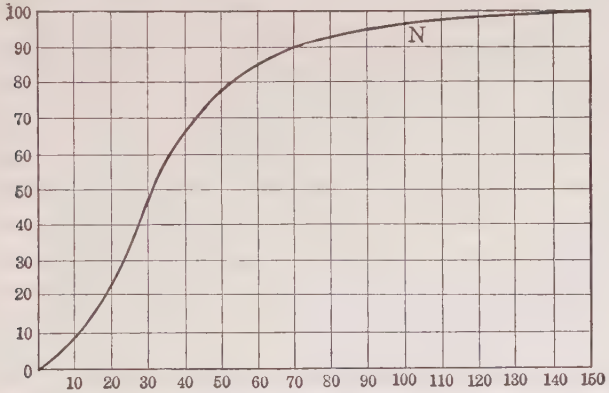


FIG. 127.—Curve to show the percentage saturation of hemoglobin with oxygen at various oxygen tensions. Figures on the left vertical line represent percentages of saturation; on the base line oxygen tensions. *N*, point indicating percentage saturation at the oxygen tension of ordinary arterial blood.

curve showing the percentage saturation, in other words, the proportion of oxyhemoglobin, at all oxygen tensions from zero to that of ordinary atmospheric air (152 mm. Hg.). The curve shows that at the oxygen pressure of alveolar air, 100 mm. Hg. (which is equal to the oxygen *tension* of the plasma of arterial blood), hemoglobin is about 97 per cent saturated. This is so near complete saturation that for practical purposes we may so regard it. Then if we know the amount of hemoglobin in 100 c. c. of blood

and the amount of oxygen a given quantity of hemoglobin can take up, we can easily calculate the *oxygen content* of 100 c. c. of arterial blood. In a former chapter p. 314) the normal hemoglobin content of blood is stated to be 14 parts in a hundred. When this quantity is present the oxygen content at saturation is approximately 18.5 c. c. per 100 c. c. of blood. Assuming half the blood to be arterial, which is probably an over- rather than an under-assumption, since veins in general have larger capacity than corresponding arteries, this would indicate the total oxygen-content of arterial blood to be about 550 c. c. (3,000 c. c. arterial blood times 0.185 c. c. oxygen per c. c. blood).

The General Oxygen Interchanges in the Blood. Suppose we have a quantity of arterial blood in the aorta. This, fresh from the lungs, will have its hemoglobin practically saturated with oxygen and in the state of oxyhemoglobin. In the blood-plasma some more oxygen will be dissolved, viz., so much as answers to a tension of that gas equal to 100 mm. Hg., which is the partial pressure of oxygen in the pulmonary alveoli. This tension of the gas in the plasma will be more than sufficient to keep the hemoglobin from giving off its oxygen. Suppose the blood now enters the capillaries of a resting muscle. In the liquid moistening this organ the oxygen tension is low, probably between 25 and 50 mm. Hg., since the tissue elements are steadily taking the gas up from the fluid around them. Consequently, through the capillary walls, the plasma will give off oxygen, and as the tension of that gas in it falls some of the oxyhemoglobin is decomposed; the oxygen thus liberated is dissolved in the plasma, whence it passes in turn to the fluid outside; and so the process continues as long as the blood is in the capillaries of the muscle.

Perhaps partly on account of the shortness of time of the stay of a given drop of blood in the capillaries, usually between one and three seconds, but mainly because there is some oxygen tension in the tissue fluids surrounding the capillaries, not all the oxyhemoglobin decomposes while the blood is passing through the capillaries. The average oxygen tension of *venous blood*, *i. e.*, blood that has passed through the capillaries, is about 50 mm. Hg. At this tension, as reference to figure 127 will show, the percentage saturation of hemoglobin is between 70 and 80, giving for the average quantity of oxygen in the venous blood of the resting Body, about

14 c. c. per 100 c. c. blood, or 420 c. c. for the total estimated quantity of venous blood. Adding this to the estimated amount of oxygen in arterial blood as given above, we have a total oxygen content of the blood, and so practically of the whole Body, of about 970 c. c.

The venous blood, returning to the heart, is pumped on into the pulmonary capillaries. Here, the partial pressure of oxygen in the alveoli being about 100 mm. Hg., and that in the plasma not over about 50, oxygen will be taken up by the latter, and as the tension of the gas rises in the plasma hemoglobin combines with it in larger and larger proportion, until the situation with which we started is restored.

Oxygen Interchanges in Active Exercise. In using the muscles vigorously we far outstrip the ability of the blood to provide the oxygen theoretically needed, and so force the Body to "go into debt for oxygen" (p. 120). In view of this fact it is interesting to inquire what the maximum oxygen-carrying capacity of the blood is. We learned in Chapter XX (p. 368) that during vigorous exercise the heart may conceivably discharge as much as 36 liters (36,000 c. c.) per minute from each ventricle, approximately a fivefold increase from the output in rest. All this volume pours through the capillaries of the lungs. At the same time the breathing is much augmented (p. 428); to a sufficient extent, indeed, so that in spite of the much greater quantity of hemoglobin that is taking up oxygen the partial pressure of the gas in the alveolar air continues to be kept at or slightly above 100 mm. Hg. The blood is pouring through the pulmonary capillaries, however, about five times as fast as in rest; the hemoglobin does not have time, therefore, to become as nearly saturated as it theoretically might. The percentage falls to about 93, instead of 97 as in the resting Body. This cuts down the oxygen-content of each 100 c. c. of blood from 18.5 c. c. to about 17 c. c. The oxygen-content of the 36 liters of blood that pass around the circulation each minute is therefore about 6 liters. This amount would be available for the tissues if they could abstract from the arterial blood all its load of oxygen. As a matter of fact, however, they do not do this. The flow through the tissue capillaries is so rapid in exercise that even though the oxygen tension in the tissues falls to zero, permitting in theory a complete decomposition of the oxyhemoglobin, some of it escapes

decomposition, and goes on into the venous blood. The greatest actual consumption of oxygen in man in one minute yet recorded is 4.6 liters, seen in an oarsman at the height of effort. As compared with the resting consumption this represents about a twelvefold increase.

The Carbon Dioxid of the Blood. The physiological oxidations going on in the tissues consume oxygen continuously and give rise to carbon dioxid and water. Under most bodily conditions about one-fifth of the volume of oxygen taken up is accounted for in the water formed, and four-fifths in the carbon dioxid (this should not be interpreted to mean that atmospheric oxygen actually combines with hydrogen and carbon in those proportions; compare p. 25). The exact ratio between the carbon dioxid exhaled and the oxygen inhaled varies with the fuel burned, sugar giving a higher ratio than fat. The carbon dioxid formed in the tissues is conveyed from them in the blood to the lungs and there passed out into the alveolar air to be carried to the exterior in the expired air.

We have already learned that much of the carbonic acid (carbon dioxid plus water) is present in the blood in the form of sodium bicarbonate (p. 425). The reason for this is found in a fundamental principle of chemistry, known as the *mass law*, which can be illustrated for our present purpose by using the substances actually concerned in blood. The chief inorganic constituent of blood is, as already pointed out, sodium chlorid. When this and carbonic acid are present together in the same solution they react to form sodium bicarbonate and hydrochloric acid according to the equation: $NaCl + H_2CO_3 \rightleftharpoons NaHCO_3 + HCl$. Since all these substances are soluble they exist together in the blood-plasma; but under the conditions present in plasma the reaction comes to equilibrium with relatively only a small formation of bicarbonate and hydrochloric acid; the left hand members of the equation will be greatly in excess of the right hand. In order to bring about the conversion of large amounts of carbonic acid to bicarbonate the hydrochloric acid must be removed somehow from the solution; if this can be done the reaction will go on, with formation of bicarbonate, as long as the carbonic acid and sodium chlorid hold out.

In the blood removal of hydrochloric acid is accomplished by means of the red corpuscles, which have a large capacity for acid. To picture the situation as it exists in our blood we have to imagine

the plasma at some past time as completely free from carbonic acid, bicarbonate, and hydrochloric acid, but containing its full quota of sodium chlorid. The tissues are carrying on their normal metabolism, consequently they produce and pour out into the plasma carbon dioxid, which immediately forms carbonic acid by union with water. This acid then reacts with sodium chlorid according to the above equation, forming sodium bicarbonate and hydrochloric acid. Since the capacity of the red corpuscles for hydrochloric acid is at this time untouched they take up all that is formed; thus permitting all but a trace of the carbonic acid to change to bicarbonate. This goes on till the capacity of the red corpuscles for hydrochloric acid approaches exhaustion, when the situation existing in our blood is established. In other words, we have about all the hydrochloric acid our red corpuscles can hold, and therefore nearly all the bicarbonate in our plasma the above reaction will permit.

Let us now refer to the account of the control of breathing given in the last chapter. We saw there that the increase of acidity of the respiratory center above the critical level depends on such an accumulation of carbonic acid in the plasma that its escape from the cells of the center is hampered. From what we learned in the paragraph above it is clear that carbonic acid cannot accumulate to any extent in the plasma so long as its conversion to bicarbonate is taking place. Only as the red corpuscles approach the limit of their capacity for hydrochloric acid does carbonic acid tend to remain as such in the plasma; hence the respiratory center does not become acid enough to be excited until the same limit is approached. The concentration of sodium bicarbonate in our blood is evidently determined, therefore, by the capacity of our red corpuscles for hydrochloric acid.

Hemoglobin Holds more Acid than Oxyhemoglobin. One more fact about the acid capacity of the red corpuscles must be stated before going on to the consideration of the transport of carbon dioxid from tissues to alveolar air. This is that arterial blood, *i. e.*, blood whose red corpuscles contain nearly all oxyhemoglobin, and very little hemoglobin in reduced form, has less capacity for acid than venous blood, in which considerable hemoglobin is present as such. The difference is due to a difference in alkalinity between hemoglobin and oxyhemoglobin, the former being more

alkaline than the latter (the term alkaline is used here as meaning acid-holding capacity rather than reaction).

The Transport of Carbon Dioxid. We may now turn to consider how the Body rids itself of carbon dioxid as fast as formed. The source of carbon dioxid is in the tissue cells; from them it dialyzes into the surrounding tissue fluids, and thence into the blood-plasma, provided the latter has a lower carbon dioxid tension than the tissue fluids themselves. The carbon dioxid tension of plasma is to all intents and purposes equivalent to the carbonic acid concentration of the same (the equilibrium between dissolved carbon dioxid and carbonic acid is too complicated for discussion here). On account of the fact that the acid-holding capacity of the red corpuscles is not entirely exhausted in ordinary arterial blood the carbonic acid concentration of that blood as it enters the tissue capillaries is low; consequently there is a flow of carbon dioxid from tissue fluids to blood-plasma. The fact that in these capillaries oxyhemoglobin is changing to hemoglobin helps also, since the red corpuscles become able to hold more acid just at the instant when more is being presented to them. The effect of the influx of carbon dioxid into the plasma is to increase the amount of carbonic acid present in it; the reaction on p. 446 accordingly takes place, raising the concentration of bicarbonate somewhat, and bringing the red corpuscles nearer their acid-holding limit than before. Furthermore, since the latter are very close to their limit anyway, there is an actual increase in the amount of carbonic acid present. In venous blood, therefore, there is more bicarbonate in the plasma, more acid in the red corpuscles, and more carbonic acid in the plasma than in arterial blood. The actual *tension* of carbon dioxid is about 45–50 mm. Hg. in venous blood; the total amount, including that present both as carbonic acid and bicarbonate, is, as already stated (p. 439) about 54.4 c. c. per 100 c. c. blood.

When this blood enters the capillaries of the lungs it comes into exchange relationship with alveolar air. Normal breathing maintains a degree of lung ventilation such that the carbon dioxid pressure of the alveolar air rarely rises above 40 mm. Hg. There is therefore a sufficient *diffusion gradient* between venous blood and alveolar air to cause carbon dioxid to pass outward. Furthermore, the change of hemoglobin to oxyhemoglobin in the same

capillaries acts to expel some acid from the corpuscles, raising the tension of acid in the plasma, and helping the diffusion to that extent.

The reaction: $NaCl + H_2CO_3 \rightleftharpoons NaHCO_3 + HCl$ is *reversible;* that is, if the quantity of one of the left-hand constituents is reduced, the reaction goes backward, bicarbonate and hydrochloric acid reacting to form carbonic acid and sodium chlorid. This happens when carbon dioxid begins to diffuse out from the blood to the alveolar air; the resulting reduction in the amount of carbonic acid leads to the decomposition of bicarbonate to form more, which in turn passes by diffusion as carbon dioxid out of the blood. A corresponding passage of hydrochloric acid out of the red corpuscles necessarily occurs. Thus in the plasma of arterial blood there is less bicarbonate and less carbonic acid, and in the red corpuscles less hydrochloric acid, than in the venous blood.

As the result of these changes the blood leaving the pulmonary capillaries (arterial blood) has its carbon dioxid tension lowered to about that of alveolar air, *i. e.*, 40 mm. Hg., and its total content of carbon dioxid to about 50 c. c. per 100 c. c. of blood. Assuming a blood-flow per minute of 7,400 c. c. (p. 368), the elimination of carbon dioxid for the same period figures out at about 325 c. c.

Carbon Dioxid Elimination in Exercise. The production of carbon dioxid in vigorous exercise increases somewhat more rapidly than does the oxygen consumption. This is because as the Body "goes in debt for oxygen" it forms lactic acid, which reacts with sodium bicarbonate to form sodium lactate and carbon dioxid. Thus whenever sodium lactate is accumulating there is not only the carbon dioxid formed by direct oxidation in the tissues but also that formed from bicarbonate by the action of lactic acid. Since the increase in oxygen consumption may be about twelvefold (p. 446), the increase in carbon-dioxid production may presumably be thirteenfold or more. To care for this we have a fivefold increase in blood-flow (p. 368). Evidently each c. c. of blood must also carry carbon dioxid about two and a half times as effectively as during rest. This means that the difference in total carbon dioxid content between arterial and venous blood must be about 11–12 c. c. per 100 c. c. of blood, instead of 4.5 c. c. as in rest. In the main this is brought about by an increase in the uptake of carbon dioxid by venous blood. The more complete decomposition

of oxyhemoglobin in active tissues makes the blood correspondingly more alkaline, and so increases its capacity for carbonic acid; there is, besides, a definite increase in the amount of uncombined carbonic acid in the venous blood, as shown by the more vigorous discharges of the respiratory center; this latter increase implies also some increase in the amount of bicarbonate formed, since the red corpuscles are not absolutely at their acid-holding limit in ordinary venous blood, and so can permit the bicarbonate-forming reaction to proceed somewhat further. There is probably also usually some reduction in the amount of carbon dioxid in the arterial blood, since the lung ventilation nearly always is somewhat excessive in vigorous exercise, in that it lowers the carbon-dioxid pressure of alveolar air a little below 40 mm. Hg., which is its normal level in the quiet Body. The combined result is to eliminate from the Body all the carbon dioxid formed, even in violent exercise. Since this is so we have to look to some other cause for the violent respiratory distress and the exhaustion that attend such exercise. This we have in the outpouring of sodium lactate. It appears that if the exercise is so gauged that the oxygen supply keeps full pace with the tissue requirements there is little or no difficulty with the breathing, and only gradual onset of fatigue. Respiratory distress is probably a sure indication that the Body is "going into debt for oxygen."

Coal Gas Poisoning. In the paragraph on anoxemia (Chap. XXIII) the possibility of suffocation by carbon monoxid was mentioned. This substance, which is an important constituent of illuminating gas, has a greater affinity for hemoglobin than has oxygen, and forms with it a more stable compound, *carbon monoxid hemoglobin*. The result of breathing illuminating gas is, then, the conversion of hemoglobin of the blood into carbon monoxid hemoglobin, and the consequent abolishment of the oxygen-carrying function of the red corpuscles. The resulting anoxemia is more or less severe according to the proportion of carbon monoxid in the air breathed, since if oxygen is being breathed also at the same time it combines with part of the hemoglobin. The latter is partitioned between the two gases that combine with it in proportion to their relative affinities, and also in proportion to the quantities of each present. It follows from this last that if a victim of gas poisoning is removed promptly enough to pure air, or better yet,

given pure oxygen to breathe, the carbon monoxid can all be displaced from the hemoglobin, restoring the oxygen-carrying capacity of the blood completely. The ill-effects, often long drawn out, that follow severe gas poisoning are wholly due to the deprivation of oxygen suffered by certain tissues, chiefly nervous. They illustrate emphatically how dependent these tissues are, for healthy normal functioning, upon constant adequate supplies of oxygen, so that the physiological oxidations, of such importance in their metabolism, shall not fail or be unduly diminished.

CHAPTER XXV

FOODS: THEIR CLASSIFICATION

What Constitutes Food. Material is taken into the Body in three physical states: solid, liquid, gaseous. We have considered the gaseous intake under the head of respiration, and turn now to the use by the Body of solid and liquid substances. From the standpoint of physiology we may include under the head of food everything, either solid or liquid, which is taken into the Body and used there for its normal functioning. This classification includes with the foods liquid substances, such as milk and water, which we ordinarily classify separately as drinks. It is clear, however, that from the standpoint of the Body a classification on this basis, the physical nature of the substance taken, is not very helpful, and we shall therefore disregard the distinction commonly made between liquid and solid foods.

The Function of Food. If we have got the viewpoint which the earlier chapters of this book have attempted to instill, and are able to look upon the Body as a piece of machinery, we appreciate that materials must be furnished it for at least two purposes: (1) to supply what it needs for the liberation of energy; and (2) to provide for its maintenance and repair. The first of these requirements is a simple fuel demand; anything that the Body is able to oxidize can be used if its burning or mere presence does not injure the delicate machinery. The second requirement is not so simple; the repair of the complex Body mechanism calls for particular repair materials; in the carrying on of the Body's functions there is a continuous loss from it of substances, such as water, which must be continuously replaced; moreover, we often see fit to introduce substances which we think will aid the Body in carrying out its functions, as coffee, tea, spices, and condiments.

In the case of the child an additional factor enters, namely, *growth*, or the manufacture of new tissue. As we have seen, this is not precisely equivalent to the repair of tissue already present, so that we shall have also to consider foods in their relationship to growth.

Classes of Foods. We are aware that the materials which compose our meals include indigestible substances as well as true foods. These indigestible materials serve, as we shall see, an important function through the bulk they impart to the food; it would be extremely difficult to maintain the Body in health upon a diet from which they were excluded; we may borrow for them an expressive term used by feeders of cattle for bulky stuffs of little nutritive value, and designate them as *roughage*.

The true foods fall into two classes, *energy yielders* and *non-energy yielders*. The latter class includes all the *inorganic* constituents of the diet, such as water and the various salts; and a number of organic substances which serve definite purposes not involving the liberation of energy by them. These non-energy yielders are commonly classed as *accessories* of the diet, to signify their subordinate relation to the energy-yielding food. We have to recognize, however, that some of the so-called accessories are necessary to health. These we may call the *essential* accessories. They include water, the various salts, and a group of organic substances previously mentioned (p. 27), and to be described in detail in later paragraphs known as the *vitamins*. The other accessories of the diet, chiefly organic, may be designated as *occasional* accessories. Among these are included the special substances which give flavor to the food, and by making it palatable aid in its digestion. All drugs, including the essential principles of tea, coffee, and cocoa, fall also into this class, as do the substances classed as *condiments*, pepper, mustard, etc.

The organic constituents of our food not included among the group of accessory articles of diet belong chemically to one or other of the three great subdivisions mentioned in Chapter I. They are either *carbohydrates*, *fats*, or *proteins*. The entire supply of energy for the Body, and its repair and maintenance to great extent are derived from these three classes of food stuffs. Because of their prime importance they are usually set apart from the other foods as *nutrients* proper.

Occurrence of Nutrients in Food. The articles which in common language we call foods are, in most cases, mixtures of several nutrients with inorganic and organic accessory substances and with roughage. Bread, for example, contains water, salts, gluten (a protein), some fats, much starch, and a little sugar; all true

food stuffs: but mixed with these is a quantity of *cellulose* (the chief chemical constituent of the walls which surround vegetable cells), and this is not a true food for man since it is incapable of digestion by him, except to a slight extent described below (p. 494). Chemical examination of all the common articles of diet shows that the actual number of important food stuffs is but small: they are repeated in various proportions in the different things we eat, mixed with small quantities of different flavoring substances, and so give us a pleasing variety in our meals; but the essential substances are much the same in the fare of the workman and in the "delicacies of the season." These primary food stuffs, which are found repeated in so many different foods, belong to one or the other of the classes of nutrients mentioned above; and the food value of any article of diet depends on them far more than on the traces of flavoring matters which cause certain things to be especially sought after and so raise their market value. We cannot, however, conclude that the possession of flavor by foods is wholly unnecessary. We shall see it plays a very real and very important rôle in our use of foods in general.

The Inorganic Essential Accessories. Two inorganic substances, water and sodium chlorid (common salt), are taken separately and consciously as constituents of the diet. We require such large amounts of these substances that they have to be taken thus purposely to insure that enough be got. The other inorganic materials, the chlorids, phosphates, and sulphates of potassium, magnesium, and calcium, occur in most ordinary articles of diet, so that we do not swallow them in a separate form. Phosphates, for example, exist in nearly all animal and vegetable foods; moreover, certain foods, as casein, contain phosphorous in combinations which in the Body yield it up to be oxidized to form phosphoric acid. The same is true of sulphates, which are partially swallowed as such in various articles of diet, and are partly formed in the Body by the oxidation of the sulphur of various proteins. Calcium salts are abundant in bread and milk, and are also found in many drinking-waters. That these salts are essential to life is proven by the results of feeding animals on diets which have been carefully made salt-free, but are otherwise fully adequate. Such diets invariably cause a steady decline, and, if not discontinued, death. The remarkable fact is that under these

circumstances death comes much sooner than in complete starvation, if there is no lack of water. When starvation threatens the Body conserves all its substances carefully. This power is not shown when the only elements lacking are the salts. The Body then continues to eliminate them at the usual rate along with the waste products of bodily metabolism, and a fatal deficiency comes on quickly.

Water, which is one of the two inorganic substances taken deliberately, is formed to a considerable extent in the Body as the result of the oxidation of hydrogen and also through some other metabolic reactions. This so-called *water of metabolism* amounts in man to about 400 grams (8/9 lb.) per day on the average. On an ordinary mixed diet we take in about twice the above amount unconsciously in the food, which is never actually water-free, and usually contains half or more of its weight in the form of water. The only reason we have to drink water in addition is because our daily losses from the various channels of elimination (chiefly sweat-glands, kidneys, and lungs) amount to more than the above two quantities together. The loss varies so much from day to day, as does also the intake in the food, that no satisfactory average figure for the direct water consumption can be given. Furthermore, as will be shown later, the Body has a very large capacity for eliminating excessive amounts of water taken in above actual requirements. Perhaps 800–900 grams (about a quart) is as good an average figure for daily water consumption as can be stated.

There are many desert animals that, as is well known, never drink at all. This is true of forms as high in the scale and as large and active as sheep and goats. The explanation is simply that in these forms the daily loss of water does not exceed the combined water of metabolism and the intake of water in the quite dry food, hence no deliberate drinking is necessary.

There is some loss of sodium chlorid continuously through the kidneys, necessitating that it be included in the diet. The amount thus needed is small, however, and is nearly satisfied by the normal sodium chlorid content of flesh. In fact on a complete meat diet there is little need of eating salt.

In general the craving for salt is associated with a vegetable diet. This is shown very strikingly in the case of grazing animals

that in the wild state are known to travel long distances in quest of "salt licks." Carnivorous animals, on the other hand, not only have no craving for salt, but will reject food containing an excess of it. This is said to be true also of Eskimos, whose diet is exclusively of flesh.

The relationship of the salt craving to a vegetable diet is explained on the basis of the high potash content of vegetables. The potash salts react in the Body with the sodium chlorid, forming compounds which are rapidly eliminated by the kidneys. This constant drain on the sodium chlorid of the Body gives rise to a craving which insures its adequate replenishment. We must admit, nevertheless, that civilized man habitually consumes much more salt than is absolutely necessary. The excess should be classed as a condiment, among the occasional accessories.

Vitamins. Much attention has been devoted of recent years to these interesting dietary accessories. Considerable information about them has been gained, although we know nothing as yet about the method of their action. What we do know is that they are essential to normal metabolism, so that diseases of one kind or another develop if one or another vitamin is deficient in the diet. With a single exception (see p. 458) all the vitamins so far known are of plant origin, and must be obtained by animals in their food. They are not destroyed in the animal body, however, and may be stored within certain tissues for a considerable time, or may be passed into eggs or milk; hence by eating these, animals may get their needed vitamins at second hand. While waiting definite knowledge as to the chemical structure of individual vitamins the practice has been adopted of assigning letters of the alphabet to them. So far the first five letters have been thus assigned.

Vitamin A is formed in the actively growing portions of plants and taken up by grazing animals from thence. In the animal body it is found always in association with fat, hence is known as a *fat-soluble* vitamin. It is a complex compound of carbon, hydrogen, and oxygen, but contains no nitrogen. Egg-yolk, milk-fat, and cod liver oil contain particularly high concentrations of A.

Animals cannot maintain good nutritive condition if deprived of vitamin A; they go into a state of decline in which they show marked susceptibility to certain types of infection (an eye disease

almost invariably develops in laboratory animals on an A-free diet). Death results from prolonged complete deprivation. Young animals show marked retardation of growth when fed a diet deficient in A. The effect is so marked as to have earned for this vitamin the title of the *growth-promoting* vitamin, although it is by no means sure that the vitamin affects the growth processes directly; the retardation may be simply an indirect effect of the general malnutrition attendant on A-deficiency. To insure that growing children obtain ample supplies of vitamin A they should be fed eggs, whole milk or cream, and butter (not butter substitutes made of vegetable fats). The occasional administration of cod liver oil helps also, although the prime reason for dosing with that compound is not for its content of A, but for another vitamin it contains (see under D below).

Vitamin B. This vitamin was discovered in connection with studies of a type of neuritis, known as *beriberi*, which became prevalent among certain rice-eating peoples when they began to substitute on a large scale rice hulled clean by power machinery for the same cereal hulled in cruder fashion, and so less completely, in the village or home. It was found that the disease could be prevented, or cured after becoming established, by adding water extracts of rice hulls to the diet in small amounts. This was the first of the vitamins to be discovered; it is a nitrogen-containing compound, belonging chemically to the class of *amines*. (The name "vitamine," used for some years to designate all the organic accessories of this type, was coined with the idea in mind that they all belong to the same chemical class. With the discovery that several of them are not "amines"—indeed not nitrogen compounds at all—the final *e* was dropped from the name, to avoid the implication that they are certain kinds of compounds, and yet preserve a familiar terminology.) Vitamin B is *water-soluble;* it occurs abundantly in yeast, in the hulls of grain, and in the green parts of plants. The bodies of animals contain very little of it in storage, hence carnivorous animals do not obtain an abundant supply, except as they nibble grasses as cats frequently do. Eggs and milk are fairly rich in B, however, showing that the vitamin passes into these from the maternal bodies.

Persons on an ordinary mixed diet rarely suffer such deficiency of B as to develop beriberi; they may, however, display other

symptoms indicative of insufficiency. Marked among these is loss of appetite. A very curious fact is that almost complete indifference to food may follow deprivation of B. It is probable that the undernutrition often attributed to B-deficiency is really due to the poor appetite it engenders, and only indirectly to lack of the vitamin itself. Fresh milk, green food stuffs, such as lettuce, and if these do not suffice, a cake or so of yeast a day, afford the Body the needed amounts of vitamin B.

Vitamin C is the antiscorbutic (scurvy-preventing) vitamin. From time immemorial sailors on long voyages, and others so placed as to become dependent on salt meat and hard-tack, have suffered from scurvy. Also for a very long time it has been known that scurvy can be cured by eating almost any kind of fresh fruit, and most fresh vegetables. Vitamin C is *water-soluble;* it is particularly abundant in the juice of oranges, lemons, and tomatoes, also in growing shoots and immature vegetables. If the food of cows happens to be largely of fresh grass their milk will contain C in plenty, but on hay and grain it contains little or none. This is important because infants suffer frequently from a form of scurvy when not given sufficient C. As we have just seen, cows' milk may or may not contain it: indeed the same is true of mother's milk, according to whether her diet contains fresh fruit or not. The practice of giving infants orange juice owes its value to the presence of vitamin C, although curiously the practice arose before the facts about the vitamin became known.

Vitamin D, the antirachitic vitamin, has already been described (p. 57). We need here emphasize only the point that since this vitamin may be generated in almost any animal or vegetable fat by exposure to ultra-violet radiation, it may or may not be of plant origin. All the other vitamins, so far as known, are exclusively of plant origin.

Vitamin E. A few years ago the important discovery was made that the proper carrying out of the reproductive process in laboratory animals, notably white rats, depends on the presence of a vitamin in the diet. This vitamin, designated as *E*, is present in the germ of wheat and some other grains, but in no other part of the grain, in lettuce and alfalfa, to a slight extent in milk-fat, and presumably in other foods not yet studied. There is evidence that the germinal tissues suffer impairment when the diet is deficient

in E; another striking fact is that the embryos may appear to start normal development within the uterus of the mother, but when E is deficient they die in course of time and are reabsorbed into the maternal body. The explanation of this phenomenon has yet to be found.

It is probable that still another vitamin is responsible for the occurrence of a deficiency disease, pellagra, seen in persons eating a diet too exclusively of maize. This vitamin has not been studied extensively as yet, and no letter has been assigned to it.

Occurrence of Occasional Accessories in Food. Variety in the diet depends practically altogether upon the occasional accessories, for the primary food stuffs are few in number and for the most part without very pronounced tastes or flavors, with the single exception of sugar, whose sweet taste makes it, to the eyes of most children at least, the most desirable of all foods. To civilized man variety of diet is a virtual necessity; the accessories, therefore, are to him of great importance. Both meats and vegetables owe their characteristic flavors, in the main, to organic substances present in them. We do not, however, depend wholly on these substances for securing the needed variety in our food. Condiments, pepper and mustard for example, and spices are used very largely in all civilized countries. Chocolate, coffee, and tea are taken by most people as much for their agreeable flavor as for their stimulating properties.

The Nutrients. The actual nourishment of the Body depends, as stated above, primarily upon the taking of sufficient quantities of the nutrients proper. Of the three groups of nutrients two, *carbohydrates* and *fats*, are exclusively energy yielders. Their function is to be oxidized in the Body and thus to furnish the energy by which it carries on its metabolism. The third nutrient group, the *proteins*, furnishes the material by which waste of living tissues is made good, and provides likewise a very considerable proportion of the fuel supply of the Body. Because of the twofold function of proteins it is possible for a person or animal to live for a long time upon an exclusively protein diet. Since repair of tissue waste can be made only by proteins, an animal or a man would starve to death upon a protein-free diet, no matter how much of the other food stuffs he might have.

The chemical nature of the nutrients is sufficiently described in

Chapter I; the reader may refresh his memory by reference to that chapter at this point.

Mixed Foods. These, as already pointed out, include nearly all common articles of diet; they contain more than one nutrient. Among them we find great differences; some being rich in proteins, others in starch, others in fats, and so on. The formation of a scientific dietary depends on a knowledge of these characteristics. The foods eaten by man are, however, so varied that we cannot do more than consider the most important.

Flesh. This, whether derived from bird, beast, or fish, consists essentially of the same things—muscular fibers, connective tissue and tendons, fats, blood vessels, and nerves. It contains several proteins, especially myosin and myogen (p. 98); gelatin-yielding matters in the white fibrous tissue; stearin, palmatin, and olein as representatives of the fats; and a small amount of carbohydrates in the form of glycogen and glucose, or some chemically allied substances. Flesh also contains much water and a considerable number of salines, the most important and abundant being potassium phosphate. The nitrogenous extractives (Chap. I) give much of its taste to flesh; and small quantities of various of these substances exist in different kinds of meat. There is also more or less yellow elastic tissue in flesh; it is indigestible and useless as food.

When meat is cooked its white fibrous tissue is turned into gelatin, and the whole mass becomes thus softer and more easily disintegrated by the teeth. When boiled some of the protein matters of the meat pass out into the broth, and there in part coagulate and form the *scum;* this loss may be prevented in great part by putting the raw meat at once into boiling water which coagulates the surface protein before it dissolves out, and this keeps in the rest, while the subsequent cooking is continued slowly. In any case the myosin, being insoluble in water, remains behind in the boiled meat. In baking or roasting, all the solid parts of the flesh are preserved and certain agreeably flavored bodies are produced, as to the nature of which little is known.

Eggs. These contain a large amount of egg albumen and, in the yolk, another protein, known as vitellin. Also fats, and a substance known as *lecithin*, which is important as containing a considerable quantity of phosphorus. Lecithin, or rather a substance yielding it, is an important constituent of the nervous tissues.

Milk contains at least two proteins, *lactalbumin* and *casein;* several fats in the *butter;* a carbohydrate, *milk-sugar;* much water; and salts, especially potassium and calcium phosphates. *Butter* consists mainly of the same fats as those in beef and mutton; but has in it about one per cent of a special fat, butyrin. In the milk the fat is disseminated in the form of minute globules which, for the most part, float up to the top when the milk is let stand and then form the *cream*. In this each fat-droplet is surrounded by a pellicle of albuminous matter; by churning, these pellicles are broken up and the fat-droplets then run together to form the butter.

Casein is soluble in water, but when acted on by *rennin*, an enzym of gastric juice (p. 491) is converted into *paracasein*, which forms an insoluble compound with the lime salts of the milk, and so is precipitated as the *curd*. Casein itself is rendered insoluble by acid; when milk is kept its sugar ferments, giving rise to lactic acid, the familiar process of souring; after this reaches a certain point the casein is precipitated as "clabber." There is sufficient difference between the two forms of curd so that cheeses made from them are quite unlike; cottage cheese, made from sour milk, cannot be "ripened" as can cheese made from milk acted upon by "rennet" in the ordinary commercial process of cheese making.

Vegetable Foods. Of these wheat affords the best; not that it contains more of any particular nutrient but because of a peculiar property of its protein. The protein of wheat is mainly *gluten*, which when moistened with water forms a tenacious mass, and this it is to which wheaten bread owes its superiority. When the dough is made, yeast is added to it, and produces a fermentation by which, among other things, carbon dioxid gas is produced. This gas, imprisoned in the tenacious dough, and expanded during baking, forms cavities in it and causes it to "rise" and make "light bread," which is not only more pleasant to eat but more digestible than heavy bread. Other cereals may contain a larger percentage of starch, but none have so much gluten as wheat; when bread is made from them the carbon dioxid gas escapes so readily from the less tenacious dough that it does not expand the mass properly. Corn and rice are valuable chiefly for their high carbohydrate content; beans and peas, on the other hand, have a high per cent of protein. Potatoes contain less actual nutriment for their weight than do any of the other important foods.

Their cheapness and digestibility have combined to give them a place in the average dietary out of all proportion to their real value. Other fresh vegetables, as carrots, turnips, and cabbages, are valuable mainly for the vitamins and salts they contain; their weight is mainly due to water, and they contain but little starch, proteins, or fats. Fruits, like most fresh vegetables, are mainly valuable for their vitamin and saline constituents, the other food stuffs in them being only present in small proportion. The cellulose which they contain makes up the major portion of the roughage of the diet, and is valuable on that account.

The Cooking of Vegetables. This is of more importance even than the cooking of flesh, since in most the main alimentary principle is starch, and raw starch is difficult of digestion. In plants starch is stored up within the walls of the plant-cells, which are of cellulose and therefore indigestible. When vegetables are cooked the contents of the cells swell, the cellulose walls are ruptured and the starch grains are set free and swollen, ready to be acted upon by the digestive mechanism of the Body.

Composition of Foods. The following table gives the percentage composition of some of the common foods:

In 100 Parts	Water	Protein	Fat	Digestible Carbohydrate	Inorganic Material
Meat	76.7	20.8	1.5	0.3	1.3
Eggs	73.7	12.6	12.1	.....	1.1
Cheese	36–60	25–33	7–30	3–7	3–4
Cow's Milk	87.7	3.4	3.2	4.8	0.7
Human Milk	89.7	2.0	3.1	5.0	0.2
Wheat Flour	13.3	10.2	0.9	74.8	0.5
Wheat Bread	35.6	7.1	0.2	55.5	1.1
Rye Flour	13.7	11.5	2.1	69.7	1.4
Rye Bread	42.3	6.1	0.4	49.2	1.5
Rice	13.1	7.0	0.9	77.4	1.0
Corn	13.1	9.9	4.6	68.4	1.5
Macaroni	10.1	9.0	0.3.	79.0	0.5
Peas and Beans	12–15	23–26	$1\frac{1}{2}$–2	49–54	2–3
Potatoes	75.5	2.0	0.2	20.6	1.0
Carrots	87.1	1.0	0.2	9.3	0.9
Cabbages	90.0	2–3	0.5	4–6	1.3
Mushrooms	73–91	4–8	0.5	3–12	1.2
Fruit	84.0	0.5	.....	10.0	0.5

In a bulletin of the U. S. Department of Agriculture more detailed analyses can be found. (Bull. 28.)

Alcohol. Perhaps no single question in physiology has aroused more discussion than that of the physiological position of alcohol. Its use from time immemorial as a beverage, and the long history of misery and crime which has followed its use to excess, make the problem of its true place one of very great practical importance.

We must recognize at the outset that alcohol has very diverse immediate effects according as it is taken in large or small amounts. The miserable spectacle presented by an intoxicated man emphasizes only too clearly the harm of excessive indulgence; on the other hand, the taking of a small quantity often leads to an appearance of heightened mental and physical ability. Both Mind and Body seem more alert than commonly. No one questions the injurious effects of large amounts of alcohol; the diversity of opinion is with reference to its use in small doses.

It has been demonstrated that alcohol in moderate amounts is oxidized in the Body with the liberation of energy, and is therefore a fuel in the true sense of the word. That it may serve as fuel is not in itself, however, justification for its use, even in small quantities. It must be shown that its direct physiological effects are not harmful to the Body, before it can be accepted as a food.

The action of alcohol in small doses appears to be chiefly upon the nervous system, and particularly upon the higher portions of the central nervous system. Its effect upon nerve-centers seems to be a depressing one; the generally accepted view that alcohol is a stimulant being based upon bodily effects which follow nerve-center depression rather than stimulation. For example, cutaneous vasodilation, with flushing of the skin, such as is commonly seen after taking alcohol, is the result of depression of the vaso-constrictor center. The rapid heart-beat, which is another usual phenomenon, results from depression of the cardio-inhibitory center. Even the sparkle of wit and repartee, which is reputed to be very marked after partaking of wine, is the result of removal of the brakes of judgment and caution through depression of those regions of the brain where these functions reside. It is intimated, in fact, that where alcoholic beverages flow after-dinner wit is ordinarily appreciated at more than its due desert, because of the depression of judgment in the brains of the hearers.

The depressing effect of alcohol upon the brain appears to be progressively from higher to lower centers. The first traits to be dulled are those acquired through precept and moral training; therefore the individual is apt to reveal his "true self," stripped of the veneer of education. With increasing indulgence in alcohol lower and lower tendencies come to the fore, set free by the depression of the higher, and ordinarily controlling ones. Thus it comes to pass that man may sink to the level of the beast.

The question of the moderate use of alcohol resolves itself, then, from a physiological standpoint, into one of the desirability of setting free the lower mental traits and activities through depression of the higher inhibitory ones. It is sometimes argued that in America where the dominant mental obsession of a considerable proportion of the population is in affairs of business the setting free of the brain from business cares during leisure hours is a virtual necessity, and that the use of alcohol is the most direct method of bringing this about. Even though we grant the first part of the argument it does not necessarily follow that the second part is to be accepted also. For the real objection to the use of alcohol, even in small quantities, is that the desire for alcohol, unlike the desire for food, increases as more is taken instead of decreasing when satiety is reached. It thus requires a stronger effort of will to leave off as more is taken, and since the alcohol at the same time depresses the power of the will the danger of overindulgence is continually present. Only where the will is sufficiently strong to set a limit and adhere rigidly to it is the continuous moderate use of alcohol in any degree safe.

Returning to the question of the desirability of the practice of removing the brakes from the brain periodically, it may be said that the opinion seems to be becoming more and more prevalent among neurologists that the use of alcohol for such a purpose, particularly in early and middle life, is more of an injury than a benefit. The normal interactions among the different parts of the mental apparatus should be permitted, according to these observers, to proceed without artificial interference, at least during the period of the most active associative processes.

A consideration that is only indirectly of physiological importance, yet has had much to do with the adoption of prohibition by the United States, is that in a civilization like ours, in which

the control and use of mechanical power is the dominant feature, interference, even on the most moderate scale, with the normal functioning of the higher brain centers becomes too hazardous to be tolerated. Where each individual, on the average, is in control of power equal to that of fifty human beings, the harm that a befuddled brain can do is, or may be, magnified beyond endurance. Since it seems to be neither equitable nor feasible to permit indulgence to those who refrain from using mechanical power, while forbidding it to those who do use such power, there appears to be no escape from the present plan of general prohibition.

Tea, Coffee, and Cocoa. These beverages all owe their special physiological properties to certain alkaloids present in them. The active principle of tea and coffee is the same, *caffein;* that of cocoa, and its derivative, chocolate, is a closely related substance, *theobromin.* Both are chemically in the class of *purin bodies,* related to uric acid (p. 22). Caffein and theobromin appear to be direct nerve-stimulants. They cause a rise of blood-pressure through stimulation of the vasoconstrictor center. Their use, like that of alcohol, constitutes an artificial interference with normal processes, and is subject, therefore, to the general objections which arise against such interference. Their effects are of varying intensity; cocoa is an exceedingly mild stimulant; tea, properly made, is somewhat stronger; and coffee, properly made, is stronger yet. Their use is borne much better by some persons than by others. They are not dangerous in the sense that alcohol is, through an increasing craving which readily leads to overindulgence and resulting disaster, although they, like alcohol, are often taken to excess. Temperance in the use of these beverages is as much the part of wisdom as in the use of alcohol. Again, like alcohol, they are best left alone during early life.

The improper preparation of tea and coffee, by boiling them in water, carries into solution, in addition to the stimulating principle, a substance, *tannin,* whose effect upon the system is apt to be distinctly harmful. These beverages should therefore always be prepared by methods which do not involve prolonged or even brief boiling while the tea leaves or coffee grounds are actually present in the liquid.

Food Poisoning. There are several conditions under which foods, instead of being of benefit to the Body, may become ac-

tually harmful. They need to be guarded against, both by individuals and by the public. The latter because, with the present organization of society, virtually all foods pass through many hands before they finally reach the consumer, and there are correspondingly many possibilities of contamination. The deliberate introduction into foods of injurious adulterants is now almost unknown, thanks to the effective enforcement of Federal and State "pure-food" laws. Unintentional contamination may occur, although it is much less likely under modern scientific conditions than formerly when rule-of-thumb methods obtained. A historical example of accidental contamination is the ergot poisoning that used occasionally to ravage certain parts of Europe. Ergot is a poisonous constituent of a parasitic growth sometimes found on rye. When the affected grain was made into rye flour and eaten regularly over a long period, whole populations underwent typical ergot poisoning. The symptoms were in many respects similar to those of leprosy; dry gangrene, with loss of fingers and toes, and ultimate death.

More dangerous, because more difficult to guard against, are chemical changes that may occur in food between the time of its preparation and its consumption. These are usually the result of bacterial growth within the food mass, this growth giving rise to toxins as waste products in much the same manner as does the growth of pathogenic organisms within the Body. There are at least two conditions of poisoning from such toxins. The first is *ptomain* poisoning; the toxins formed are known as ptomains. The chief symptom is the very pronounced gastro-intestinal upset. This is beneficial in that it acts to rid the Body promptly of the contaminated material, and so to reduce the amount of poison absorbed. A second form of poisoning from bacterial decomposition is *botulism*, so named from its occasional occurrence in sausage, although in this country it is seen usually only in improperly canned vegetables. The effect of this poison on the digestive tract is just opposite to that of ptomain. It paralyzes instead of exciting; so the poisoned mass is not expelled, but remains in the intestinal tract and allows absorption to continue. For this reason botulism has ordinarily much more serious effects than has ptomain. The toxin of botulism is destroyed by heat; consequently there is no danger if the canned food is heated before

being served. Most cases are due to the use of spoiled home-canned vegetables in salads.

An additional type of food poisoning is that seen in individual susceptibilities, or *idiosyncracies*. Some people are poisoned by veal, others by shellfish, occasionally a case of susceptibility to egg albumen is seen. Various other foods may act similarly. The poisonous elements in these cases appear to be identical with the lymphagogues described in a previous chapter (p. 406). The lymphagogue action was there stated to show itself only in susceptible individuals. In general acute poisoning is probably only a more marked manifestation of the sensitiveness which takes the form of increased permeability of the capillaries in those in whom the action is purely that of a lymphagogue.

CHAPTER XXVI

THE ALIMENTARY CANAL AND ITS APPENDAGES

General Arrangement. The alimentary canal is essentially a tube running through the Body (Fig. 2) and lined by a vascular membrane, a large part of which is specially adapted for absorption; it communicates with the exterior at three points (the nose, the mouth, and the anal aperture), at which the lining *mucous membrane* is continuous with the general outer integument. Supporting the lining membrane are layers which strengthen the tube, and are in part muscular and, by their contractions, serve to pass materials along it from one end to the other. In the walls of the canal are numerous blood and lymphatic vessels which carry off the matters absorbed from its cavity; and there also exist in connection with it numerous glands, whose function it is to pour into it various secretions by which the chemical act of digestion is carried on. Some of these glands are minute and imbedded in the walls of the alimentary tube itself, but others (such as the salivary glands) are larger and lie away from the main channel, into which their products are carried by ducts of various lengths.

The alimentary tube is not uniform but presents several dilatations on its course; nor is it straight, since, being much longer than the Body, a large part of it is packed away by being coiled up in the abdominal cavity.

Subdivisions of the Alimentary Canal. The mouth-opening leads into a chamber containing the teeth and tongue, the *mouth-chamber* or *buccal cavity*. This is succeeded by the *pharynx* or *throat-cavity*, which narrows at the top of the neck into the *gullet* or *œsophagus;* this runs down through the thorax and, passing through the diaphragm, dilates in the upper part of the abdominal cavity into the *stomach*. Beyond the stomach the channel again narrows to form a long and greatly coiled tube, the *small intestine*, which terminates by opening into the *large intestine*, much shorter although wider than the small, and terminating by an opening on the exterior.

The Mouth-Cavity (Fig. 128) is bounded in front and on the sides by the lips and cheeks, below by the tongue, *k*, and above by the *palate;* which latter consists of an anterior part, *l*, supported by bone and called the *hard palate*, and a posterior, *f*, containing no bone, and called the *soft palate*. The two can readily be distinguished by applying the tip of the tongue to the roof of the mouth and drawing it backwards. The hard palate forms the partition between the mouth and nose. The soft palate arches down over the back of the mouth, hanging like a curtain between it and the pharynx, as can be seen by holding the mouth open in front of a looking-glass. From the middle of its free border a conical process, the *uvula*, hangs down.

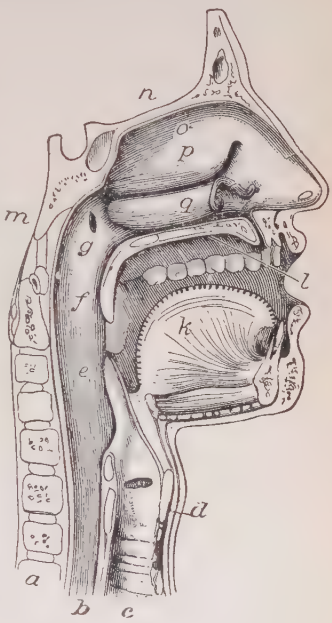


FIG. 128.—The mouth, nose and pharynx, with the commencement of the gullet and larynx, as exposed by a section, a little to the left of the median plane of the head. *a*, vertebral column; *b*, gullet; *c*, windpipe; *d*, larynx; *e*, epiglottis; *f*, soft palate; *g*, opening of Eustachian tube; *k*, tongue; *l*, hard palate; *m*, the sphenoid bone on the base of the skull; *n*, the fore part of the cranial cavity; *o*, *p*, *q*, the turbinate bones of the outer side of the left nostril-chamber.

The Teeth. Immediately within the cheeks and lips are two semicircles, formed by the borders of the upper and lower jawbones, which are covered by the *gums*, except at intervals along their edges where they contain sockets in which the teeth are implanted. During life two sets of teeth are developed; the first or *milk set* appears soon after birth and is shed during childhood, when the second or *permanent set* appears.

The teeth differ in minor points from one another, but in each three parts are distinguishable; one, seen in the mouth and called the *crown* of the tooth; a second, imbedded in the jawbone and called the *root* or *fang;* and between the two, embraced by the edge of the gum, is a narrowed portion, the *neck* or *cervix*. From differences in their forms and uses the teeth are divided into *incisors*, *canines*, *bicuspids*, and *molars*, arranged in a definite

order in each jaw. Beginning at the middle line we meet in each half of each jaw with, successively, two incisors, one canine, and two molars in the milk set; making twenty altogether in the two jaws. The teeth of the permanent set are thirty-two in number, eight in each half of each jaw, viz.—beginning at the middle line—two incisors, one canine, two bicuspids, and three molars. The bicuspids, or premolars, of the permanent set replace the milk-molars, while the permanent molars are new teeth added on as the jaw grows, and not substituting any of the milk-teeth. The hindmost permanent molars are often called the *wisdom teeth*.

Characters of Individual Teeth. The *incisors* (Fig. 129, A) are adapted for cutting the food. Their crowns are chisel-shaped and have sharp horizontal cutting edges, which become worn away

Fig. 129.

A—An incisor tooth.
B—A canine or eye-tooth.
C—A bicuspid tooth seen from its outer side; the inner cusp is, accordingly, not visible.
D—A molar tooth.

by use so that they are beveled off behind in the upper row, and in the opposite direction in the lower. Each has a long root. The *canines* (Fig. 129, B) are somewhat larger than the incisors. Their crowns are thick and somewhat conical, having a central point or *cusp* on the cutting edge. In dogs, cats, and other *carnivora* the canines are very large and adapted for seizing and holding prey. The *bicuspids* or *premolars* (Fig. 129, C) are rather shorter than the canines and their crowns are somewhat cuboidal. Each has two cusps, an outer towards the cheek, and an inner on the side turned towards the interior of the mouth. The root is compressed laterally, and has usually a groove partially subdividing it into two. At its tip the separation is often complete. The *molar teeth* or *grinders* (Fig. 129, D) have large crowns with broad surfaces, on which are four or five projecting tubercles, which

roughen them and make them better adapted to crush the food. Each has usually several roots. The *milk-teeth* differ only in subsidiary points from those of the same names in the permanent set.

The Structure of a Tooth. If a tooth be broken open, a cavity extending through both crown and root will be found in it. This

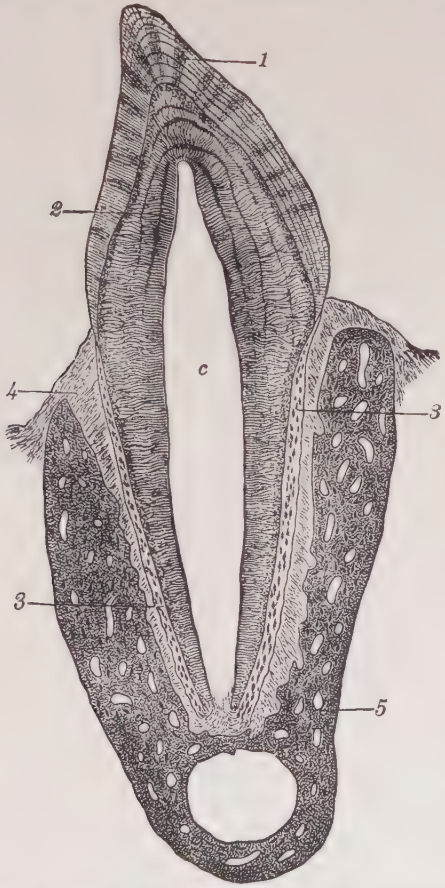


FIG. 130.—Section through a premolar tooth of the cat still embedded in its socket. 1, enamel; 2, dentine; 3, cement; 4, the gum; 5, the bone of the lower jaw; *c*, the pulp-cavity.

is filled during life with a soft vascular pulp, and hence is known as the "pulp-cavity" (*c*, Fig. 130). The hard parts of the tooth disposed around the pulp-cavity consist of three different tissues.

Of these one immediately surrounds the cavity and makes up most of the bulk of the tooth; it is *dentine* (2, Fig. 130); covering the dentine on the crown is the *enamel* (1, Fig. 130) and on the root, the cement (3, Fig. 130).

The pulp-cavity opens below by a narrow aperture at the tip of the root, or at the tip of each if the tooth have more than one. The pulp consists mainly of connective tissue, but its surface next the dentine is covered by a layer of columnar cells. Through the opening on the root blood vessels and nerves enter the pulp.

The dentine (ivory) yields on analysis the same materials as bone but is somewhat harder, earthy matters constituting 72 per cent of it as against 66 per cent in bone. Under the microscope it is recognized by the fine *dentinal tubules* which, radiating from the pulp-cavity, perforate it throughout, finally ending in minute branches which open into irregular cavities, the *interglobular spaces*, which lie just beneath the enamel or cement. At their widest ends, close to the pulp-cavity, the dentinal tubules are only about 0.005 millimeter ($\frac{1}{4500}$ of an inch) in diameter. The *cement* is much like bone in structure and composition. It is thickest at the tip of the root and thins away towards the cervix. *Enamel* is the hardest tissue in the Body, yielding on analysis only from 2 per cent to 3 per cent of organic matter, the rest being mainly calcium phosphate and carbonate. Its histological elements are minute hexagonal prisms, closely packed, and set on vertically to the surface of the subjacent dentine. It is thickest over the free end of the crown, until worn away by use. Covering the enamel in unworn teeth is a thin structureless horny layer, the *enamel cuticle*.

The Tongue (Fig. 131) is a muscular organ covered by mucous membrane, extremely mobile, and endowed not only with a delicate tactile sensibility but with the terminal organs of the special sense of taste; it is attached by its root to the hyoid bone. On its upper surface are numerous small eminences or *papillæ*, such as are found more highly developed on the tongue of a cat, where they may be readily felt. On the human tongue there are three forms of papillæ, the *circumvallate*, the *fungiform*, and the *filiform*. The circumvallate papillæ, 1 and 2 (Fig. 131), the largest and least numerous, are from seven to twelve in number and lie near the root of the tongue arranged in the form of a V with its open angle

turned forwards. Each is an elevation of the mucous membrane, covered by epithelium, and surrounded by a trench. On the sides of these papillæ, imbedded in the epithelium, are many small oval bodies richly supplied with nerves and concerned in the sense

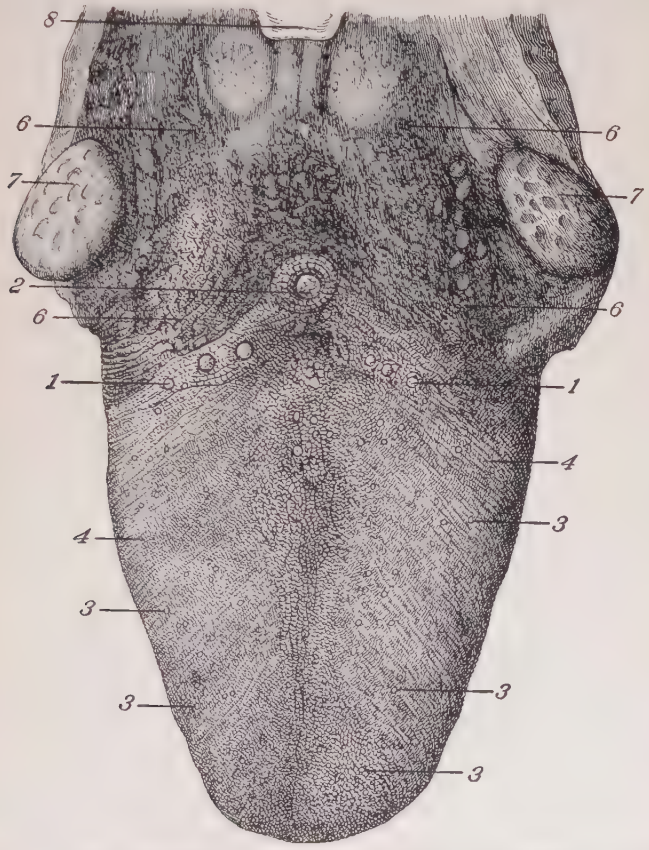


FIG. 131.—The upper surface of the tongue with part of the pillars of the fauces and the tonsils. 1, 2, circumvallate papillæ; 3, fungiform papillæ; 4, filiform papillæ; 6, mucous glands; 7, tonsils; 8, tip of epiglottis.

of taste, hence called the *taste-buds* (Chap. XIV). The *fungiform papillæ*, 3, are rounded elevations attached by somewhat narrowed stalks, and found all over the middle and fore part of the upper surface of the tongue. They are easily recognized on the living tongue by their bright red color. The *filiform papillæ*, 4, most

numerous and smallest, are scattered all over the dorsum of the tongue except near its base. Each is a conical eminence covered by a thick horny layer of epithelium. It is these papillæ which are so highly developed on the tongues of *Carnivora*, and serve them to scrape bones clean of even such tough structures as ligaments.

In health the surface of the tongue is moist, covered by little "fur," and in childhood of a red color. In adult life the natural color of the tongue is less red, except around the edges and tip; a bright-red glistening tongue being then, usually a symptom of disease. When the digestive organs are deranged the tongue is commonly covered with a thick yellowish coat, composed of a little mucus, some cells of epithelium shed from the surface, and numerous bacteria; and there is frequently a "bad taste in the mouth." The whole alimentary mucous membrane is in close physiological relationship; and anything disordering the stomach is likely to produce a "furred tongue."

The Salivary Glands. The saliva, which is poured into the mouth and which, mixed with the secretion of minute glands imbedded in its lining membrane, moistens it, is secreted by three pairs of glands, the *parotid*, the *submaxillary*, and the *sublingual*. The parotid glands lie in front of the ear behind the ramus of the lower jaw; each sends its secretion into the mouth by a tube known as *Stenson's duct*, which crosses the cheek and opens opposite the second upper molar tooth. In the disease known as *mumps* * the parotid glands are inflamed and enlarged. The submaxillary glands lie between the halves of the lower jawbone, near its angles, and their ducts open beneath the tongue near the middle line. The sublingual glands lie beneath the floor of the mouth, covered by its mucous membrane, between the back part of the tongue and the lower jawbone. Each has many ducts (8 to 20), some of which join the submaxillary duct, while the rest open separately in the floor of the mouth.

The Fauces is the name given to the aperture which can be seen at the back of the mouth below the soft palate (Fig. 128), and leading into the pharynx. It is bounded above by the soft palate and uvula, below by the root of the tongue, and on the sides by muscular elevations covered by mucous membrane, which reach from the soft palate to the tongue. These elevations are the *pil-*

* Parotitis, in technical language.

lars of the fauces. Each bifurcates below, and in the hollow between its divisions lies a *tonsil* (7, Fig. 131), a soft rounded body about the size of an almond, composed of lymphoid tissue (Chap. XXII).

The Pharynx or Throat-Cavity (Fig. 128). This portion of the alimentary canal may be described as a conical bag with its broad end turned upwards towards the base of the skull, and its narrow end downwards and passing into the gullet. Its front is imperfect, presenting openings which lead into the nose, the mouth, and (through the larynx and windpipe) the lungs. Except during swallowing or speech the soft palate hangs down between the mouth and pharynx; during deglutition it is raised into a horizontal position and separates an upper or *respiratory portion* of the pharnyx from the rest. Through this upper part, therefore, air alone passes, entering it from the posterior ends of the two nostril-chambers (*nares*); while through the lower portion both food and air pass, one on its way to the gullet, *b*, Fig. 128, the other through the larynx, *d*, to the windpipe, *c;* when a morsel of food "goes the wrong way" it takes the latter course. Opening into the upper portion of the pharynx on each side is an Eustachian tube, *g* (p. 242); so that the apertures leading out of it are seven in number; the two posterior nares, the two Eustachian tubes, the fauces, the opening of the larynx, and that of the gullet. At the root of the tongue, over the opening of the larynx, is a plate of cartilage, the *epiglottis*, *e*, which can be seen if the mouth is widely opened and the back of the tongue pressed down by some such thing as the handle of a spoon. During swallowing the epiglottis is pressed down like a lid over the air-tube and helps to keep food or saliva from entering it. In structure the pharynx consists essentially of a bag of connective tissue lined by mucous membrane, and having muscles in its walls which drive the food on.

The Esophagus or Gullet is a tube commencing at the lower termination of the pharynx and which, passing on through the neck and chest, ends below the diaphragm by joining the stomach. In the neck it lies close behind the windpipe. It consists of three coats—a mucous membrane within; next, a submucous coat of areolar connective tissue: and, outside, a muscular coat made up of two layers, an inner with transversely and an outer with longitudinally arranged fibers. In and beneath its mucous membranes

are numerous small mucous glands whose ducts open into the tube.

The Stomach (Fig. 132) is a somewhat conical bag (the precise shape is variable, depending on the state of tonus of the muscular walls) placed transversely in the upper part of the abdominal cavity. Its larger end is turned to the left and lies beneath the diaphragm; opening into its upper border, through the *cardiac orifice* at *a*, is the gullet *d*. The narrower right end is continuous at *c* with the small intestine; the aperture between the two is the *pyloric orifice*. The pyloric end of the stomach lies lower in the abdomen than the cardiac, and is separated from the diaphragm by the liver (see Fig. 1). The concave border between the two orifices is known as the *lesser curvature*, and the convex, as the *greater curvature* of the stomach. From the latter hangs down a fold of peritoneum known as the *great omentum*. It is spread over the rest of the abdominal contents like an apron. After middle life much fat frequently accumulates in the omentum, so that it is largely responsible for the "fair round belly with good capon lin'd." The protrusion *b* to the left side of the cardiac orifice, Fig. 132, is the *fundus*. The size of the stomach varies greatly with the amount of food in it; when empty it is little more than a tube; just after a moderate meal it is about ten inches long, by five wide at its broadest part.

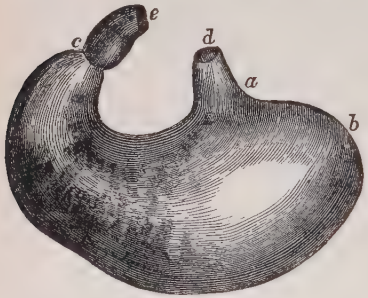


FIG. 132.—The stomach. *d*, lower end of the gullet; *a*, position of the cardiac aperture; *b*, the fundus; *c*, the pylorus; *e*, the commencement of the small intestine; along *a*, *b*, *c*, the great curvature; between the pylorus and *d*, the lesser curvature.

Since the cardiac end of the stomach lies immediately beneath the diaphragm, which has the heart on its upper side, its overdistension, due to indigestion or flatulence, may impede the action of the thoracic organs, and cause feelings of oppression in the chest, or palpitation of the heart.

Structure of the Stomach. This organ has four coats, known successively from without in as the serous, the muscular, the submucous, and the mucous. The *serous coat* is formed by a reflection of the peritoneum, a double fold of which slings the stomach; after

separating to envelop it the two layers again unite and, hanging down beyond it, form the great omentum. The *muscular coat* (Fig. 41) consists of smooth muscular tissue arranged in three layers: an outer, longitudinal, most developed about the curvatures; a circular, evenly spread over the whole organ, except around the pyloric orifice where it forms a thick ring; and an inner, oblique and very incomplete, radiating from the cardiac orifice. The *submucous coat* is made up of lax areolar tissue and binds loosely the mucous coat to the muscular. The *mucous coat* is a moist pink membrane which is inelastic, and large enough to line the stomach evenly when it is fully distended. Accordingly, when the organ is empty and shrunken, this coat is thrown into folds, which disappear when the organ is distended. During digestion the arteries supplying the stomach become dilated and, its capillaries being gorged, its mucous membrane is then much redder than during hunger.

The blood vessels of the stomach run to it between the folds of *peritoneum* which sling it. After giving off a few branches to the outer layers, most of the arteries break up into small branches in the submucous coat, from which twigs proceed to supply the close capillary network of the mucous membrane.

The nerves of the stomach belong to the autonomic system, and like most other structures supplied by this system, the stomach has double innervation (p. 208). The cranial autonomic fibers are derived from the *vagi*. In the lower part of the thorax these nerves consist mainly of nonmyclinated fibers, and lie on the sides of the gullet, across which they interchange fibers by means of several branches. On entering the abdomen the left vagus passes to the ventral side of the stomach, in which it ends: the right supplies the dorsal side of the stomach, but a considerable portion of it passes on to enter the *solar plexus*, which lies behind the stomach and contains several large ganglia. The thoracico-lumbar autonomic fibers pass to the stomach as branches from the *great splanchnic* nerves, which serve as the chief paths of distribution for these fibers in the abdomen.

Histology of the Gastric Mucous Membrane. Examination of the inner surface of the stomach with a hand lens shows it to be covered with minute shallow pits. Into these open the mouths of minute tubes, the *gastric glands*, which are closely packed side by

side in the mucous membrane; something like the cells of a honeycomb, except that each is open at one end. (It is doubtful whether the glandular structures in the pyloric region secrete true gastric juice.) Between them lie a small amount of connective tissue, a close network of lymph-channels, and capillary blood vessels. The whole surface of the mucous membrane is lined by a single layer of columnar mucus-making epithelium cells (*m*, Fig. 133). These dip down and line the necks of the tubular glands. The deeper portions of the glands are lined by a layer of shorter and somewhat cuboidal cells, the *central* or *chief* cells. In specimens taken from a healthy animal killed during digestion these cells are large and do not stain deeply with carmine. Similar specimens taken from an animal an hour or two after a good meal has been swallowed show the *chief* cells shrunken and staining more deeply. They thus store up during rest a material which they get rid of when the gastric juice is being secreted.

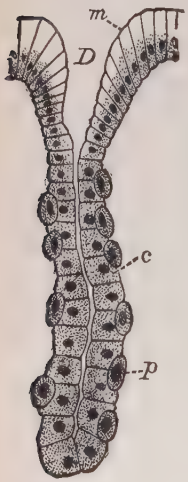


FIG. 133. — Diagram of a gastric gland. *D*, mouth of the gland; *m*, mucous cells lining the mouth of the gland and covering the inner surface of the mucous membrane; *c*, chief cells; *p*, parietal cells.

In the fundic end of the stomach only the chief cells line the glands, but elsewhere there is found outside of them, in most of the glands, an incomplete layer of larger *parietal* cells (*p*, Fig. 133). The glands frequently branch at their deeper ends.

The Pylorus. If the stomach be opened it is seen that the mucous membrane projects in a fold around the pyloric orifice and narrows it. This is due to a thick ring of the circular muscular layer there developed, and forming around the orifice a *sphincter muscle*, which, by its contraction, keeps the passage to the small intestine closed except when portions of food are being passed on from the stomach to succeeding divisions of the alimentary canal.

The Small Intestine (Fig. 140), commencing at the pylorus, ends, after many windings, in the large intestine. It is about six meters (twenty feet) long, and about five centimeters (two inches) wide at its gastric end, narrowing to about two-thirds of that width at its lower portion. Externally there are no lines of sub-

division on the small intestine, but anatomists arbitrarily describe it as consisting of three parts; the first twelve inches being the *duodenum, D,* the succeeding two-fifths of the remainder the *jejunum, J,* and the rest the *ileum, I.*

Like the stomach, the small intestine possesses four coats; a serous, a muscular, a submucous, and a mucous. The *serous coat* is formed by a duplicature of the peritoneum, but presents nothing answering to the great omentum; this double fold slinging the intestine is named the *mesentery.* The *muscular coat* is composed of plain muscular tissue arranged in two strata, an outer longitudinal, and an inner transverse or circular. The *submucous coat* is like that of the stomach; consisting of loose areolar tissue, binding together the mucous and muscular coats, and forming a bed in which the blood and lymphatic vessels (which reach the intestine in the fold of the mesentery) break up into minute branches before entering the mucous membrane.

The Mucous Coat of the Small Intestine. This is pink, soft and extremely vascular. It does not present temporary or effaceable

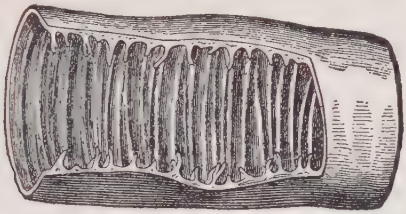


FIG. 134.—A portion of the small intestine opened to show the *valvulæ conniventes*

folds like those of the stomach, but is, throughout a great portion of its length, raised up into permanent transverse folds in the form of crescentic ridges, each of which runs transversely for a greater or less way round the tube (Fig. 134). These folds are the *valvulæ conniventes.* They are first found about two inches from the pylorus, and are most thickly set and largest in the upper half of the jejunum, in the lower half of which they become gradually less conspicuous; and they finally disappear altogether about the middle of the ileum. The folds serve greatly to increase the surface of the mucous membrane both for absorption and secretion, and they also delay the food somewhat in its passage, since it must collect in the hollows between them, and so be longer exposed to

the action of the digestive liquids. Examined closely with the eye or, better, with aid of a lens, the mucous membrane of the small intestine is seen to be not smooth but shaggy, being covered everywhere (both over the valvulæ conniventes and between them) with closely packed minute processes, standing up somewhat like the "pile" on velvet, and known as the *villi*. Each villus is from 0.5 to 0.7 millimeter ($\frac{1}{50}$ to $\frac{1}{35}$ inch) in length; some are conical and rounded, but the majority are compressed at the base in one diameter (Fig. 135). In structure a villus is somewhat complex. Covering it is a single layer of columnar epithelial cells, the exposed ends of the majority having a peculiar bright striated border and being probably of great importance in absorption. Mixed

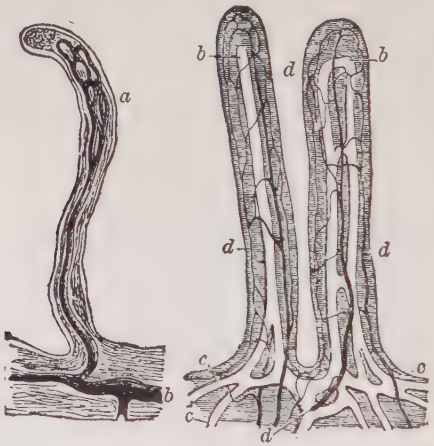


FIG. 135.—Villi of the small intestine; magnified about 80 diameters. In the right-hand figure the lacteals, *a*, *b*, *c*, are filled with white injection; *d*, blood-vessels. In the left-hand figure the lacteals alone are represented, filled with a dark injection. The epithelium covering the villi, and their muscular fibers, are omitted.

with these cells are others in which most of the cell has become filled with a clear mass which does not stain readily with reagents; the deep narrow end of the cell stains easily and contains the nucleus. From time to time the clear substance of these cells (mucigen) is converted into mucus and discharged into the intestine, leaving behind only the nucleus and the protoplasm around it. These reconstruct the cell and form more mucigen. These mucus-forming cells are named *goblet-cells*, from their shape. Beneath the epithelium the villus may be regarded as made up of a

framework of connective tissue, supporting the more essential constituents. Near the surface is an incomplete layer of plain muscular tissue, continuous below with a muscular stratum forming the deepest layer of the mucous membrane and named the *muscularis mucosæ*. In the center is an offshoot of the lymphatic system; sometimes in the form of a single vessel with a closed dilated end, and sometimes as a network formed by two main vessels with cross-branches. During digestion of fats these lymphatics are filled with a milky-white liquid absorbed from the intestines, and they are accordingly called the *lacteals*. They communicate with larger branches in the submucous coat, which end in trunks that pass out through the mesentery to join the main lymphatic system. Finally, in each villus, outside the lacteals and beneath the muscular layer of the villus, is a close network of blood vessels.

Opening on the surface of the small intestine, between the bases of the villi, are small glands, the *crypts of Lieberkühn*. Each is a simple unbranched tube lined by a layer of columnar cells some of which have a striated free border, though less marked than that on the corresponding cells of the villi, and others are goblet-cells. The crypts of Lieberkühn are closely packed, side by side, like the glands of the stomach. In the duodenum are found other minute glands, *the glands of Brunner*. They lie in the submucous coat and send their ducts through the mucous membrane to open on its inner side.

The Large Intestine (Fig. 140), forming the final portion of the alimentary canal, is about 1.5 meters (5 feet) long, and varies in diameter from about 6 to 4 centimeters ($2\frac{1}{2}$ to $1\frac{1}{2}$ inches). Anatomists describe it as consisting of the *cæcum* with the *vermiform appendix*, the *colon*, and the *rectum*. The small intestine does not open into the commencement of the large but into its side, some distance from its closed upper end, and the cæcum, *CC*, is that part of the large intestine which extends beyond the communication. From it projects the *vermiform appendix*, a narrow tube usually not thicker than a lead pencil, and averaging about 10 centimeters (4 inches) long. The colon commences on the right side of the abdominal cavity where the small intestine communicates with the large, runs up for some way on that side (*ascending colon, AC*), then crosses the middle line (*transverse colon, TC*)

below the stomach, and turns down (*descending colon, DC*) on the left side and there makes an S-shaped bend known as the *sigmoid flexure, SF;* from this the *rectum, R,* the terminal straight portion of the intestine, proceeds to the anal opening, by which the alimentary canal communicates with the exterior. In structure the large intestine presents the same coats as the small. The external stratum of the muscular coat is not, however, developed uniformly around it, except on the rectum, but occurs in three bands separated by intervals in which it is wanting. These bands being shorter than the rest of the tube cause it to be puckered, or sacculated, between them. The mucous coat possesses no villi or valvulæ conniventes, but is usually thrown into effaceable folds, like those of the stomach but smaller. It contains numerous closely set glands much like the crypts of Lieberkühn of the small intestine.

The Ileocolic Valve. Where the small intestine joins the large there is a valve, formed by two flaps of the mucous membrane sloping down into the colon, and so disposed as to allow matters to pass more readily from the ileum into the large intestine than the other way.

The Nerves of the Intestines. The intestines, like the stomach, have double autonomic innervation; the paths of approach are in general the same as for the stomach, by way of the vagus for the cranial autonomics, and the splanchnics for the thoracico-lumbar. Both these sets of nerves ramify in the *solar plexus;* from here nerve strands pass to the intestine, as well as to the stomach, along the mesentery. This innervation extends throughout the small intestine and the ascending and transverse colons. The descending colon has its thoracico-lumbar innervation by way of the *hypogastric* nerve which extends to the *hypogastric plexus* in the lower portion of the abdominal cavity and ramifies thence over the descending colon and rectum. The opposing autonomic innervation for this region is derived from the sacral part of the system. In dogs a single nerve trunk, the *nervus erigens,* is the path from the sacral part of the spinal cord to the hypogastric plexus; in man the trunk is split up into several small nerves. Thence the distribution is the same as for the thoracico-lumbar autonomics.

The intestines are provided, in addition, with an intrinsic innervation consisting of two nervous networks or plexuses lying, one between the mucosa and the muscular coat, the *plexus* of *Meissner,*

and the other between the circular and longitudinal muscle layers, the *plexus* of *Auerbach.*

The Liver. Besides the secretions formed by the glands imbedded in its walls, the small intestine receives those of two large glands, the *liver* and the *pancreas,* which lie in the abdominal cavity. The ducts of both open by a common aperture into the duodenum about 10 centimeters (4 inches) from the pylorus.

The *liver* is the largest gland in the Body, weighing from 1,400 to 1,700 grams (50 to 64 ounces). It is situated in the upper part of the abdominal cavity (*li,* Fig. 1), rather more on the right than

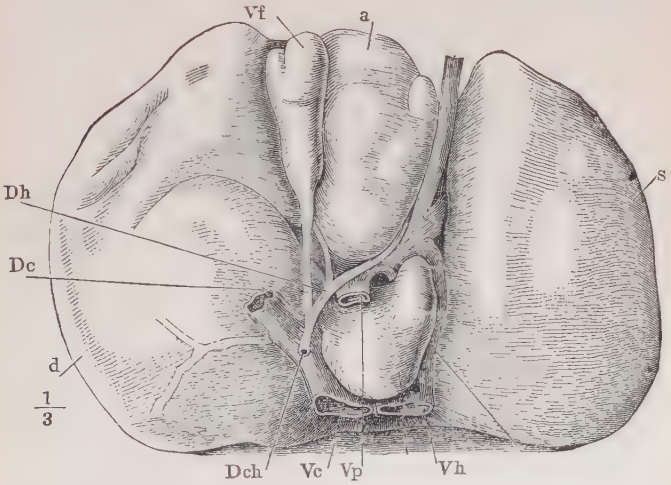


FIG. 136.—The under surface of the liver. *d,* right, and *s,* left lobe; *Vh,* hepatic vein; *Vp,* portal vein; *Vc,* vena cava inferior; *Dch,* common bile-duct; *Dc,* cystic duct; *Dh,* hepatic duct; *Vf,* gall-bladder.

on the left side and immediately below the diaphragm, into the concavity of which its upper surface fits, and reaches across the middle line above the pyloric end of the stomach. It is of dark reddish-brown color, and of a soft friable texture. A deep fissure incompletely divides the organ into *right* and *left lobes,* of which the right is much the larger; on its under surface (Fig. 136) shallower grooves mark off several minor lobes. Its upper surface is smooth and convex. The vessels carrying blood to the liver are the *portal vein, Vp,* and the *hepatic artery;* both enter it at a fissure (*the portal fissure*) on its underside, and there also a duct passes

out from each half of the organ. The ducts unite to form the *hepatic duct, Dh,* which meets at an acute angle the *cystic duct, Dc,* proceeding from the gall-bladder, *Vf,* a pear-shaped sac in which the bile, or gall, formed by the liver, accumulates. The *common bile-duct, Dch,* formed by the union of the hepatic and cystic ducts, opens into the duodenum. The blood which enters the liver by the portal vein and hepatic artery passes out by the *hepatic veins, Vh,* which leave the posterior border of the organ close to the vertebral column, and there open into the inferior vena cava just before it passes up through the diaphragm.

The Structure of the Liver. On closely examining the surface of the liver, it will be seen to be marked out into small angular

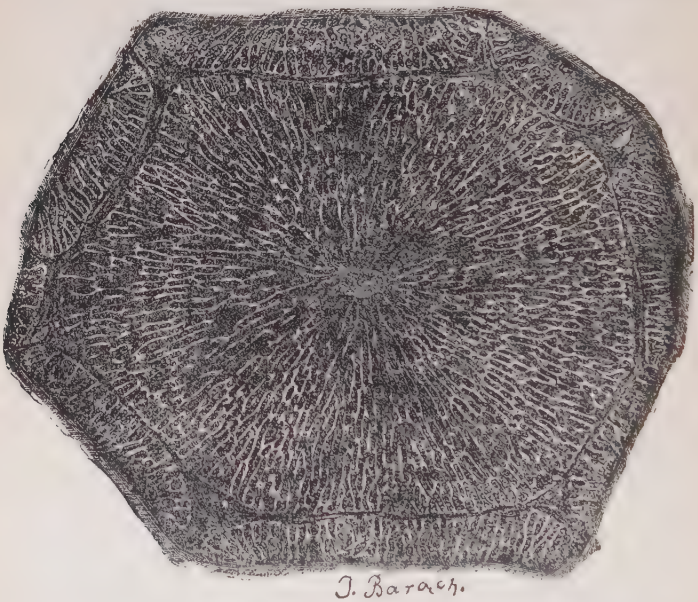


FIG. 137.—A lobule of the liver (pig), magnified, showing the hepatic cells radiately arranged around the central intralobular vein, and the connective tissue surrounding the lobule. (Scymonowicz.)

areas from one to two millimeters ($\frac{1}{25}$ to $\frac{1}{12}$ inch) in diameter. These are the outer sides of the superficial layer of a vast number of minute polygonal masses, or *lobules,* of which the liver is built up; similar areas are seen on the surface of any section made through the organ. Each lobule (Fig. 137) consists of a number

of *hepatic cells* supported by a close network of capillaries; and is separated from neighboring lobules by connective tissue, larger blood vessels, and branches of the hepatic duct. The *hepatic cells* are the proper tissue elements of the liver. Each is polygonal, nucleated and very granular, and has a diameter of about 0.025 millimeter ($\frac{1}{1000}$ of an inch). In each lobule they are arranged in rows or strings, which form a network, in the meshes of which the blood-capillaries and bile-capillaries run. The blood carried in by the portal vein (which has already circulated through the capillaries of the stomach, spleen, intestines and pancreas) becomes united on its entry into the different lobes with blood from the hepatic artery. This stream of mixed arterial and venous blood is conveyed to a fine vascular *interlobular plexus* around the liver-lobules, from which it flows on through the capillaries of the lobules themselves. These (Fig. 138) unite in the center of the lobule to form a small *intralobular vein*, which carries the blood out and pours it into one of the branches of origin of the hepatic vein, called the *sublobular vein*. Each of the latter has many lobules emptying blood into it, and if dissected out with them would look something like a branch of a tree with apples attached to it by short stalks, represented by the intralobular veins. The blood is finally carried, as already pointed out, by the hepatic veins into the inferior vena cava. The hepatic artery, which supplies about one-third the total liver blood-flow, to two-thirds supplied by the portal vein, is a direct offshoot of the celiac axis (p. 348).

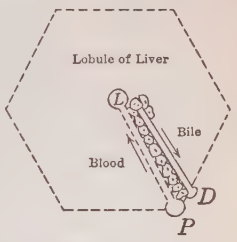


FIG. 138.—Diagram to illustrate the relationship of blood-capillaries, bile-capillaries, and liver-cells. *L*, intralobular vein at center of lobule; *P*, vessel of interlobular plexus from which a blood capillary extends to *L*; *D*, a minute bile-duct with which a bile-capillary communicates.

The bile-ducts can be readily traced to the periphery of the lobules, and there communicate with a network of extremely minute commencing bile-capillaries, ramifying in the lobule between the hepatic cells composing it. The relation of the bile-capillaries to the blood-capillaries within the lobule is such that there is always a liver-cell interposed between them. This arrangement is illustrated diagrammatically in Fig. 138.

From the arrangement of blood-capillaries and bile-capillaries with their connections we can picture the movement of blood and

bile through the lobules; the mixed blood from the portal vein and hepatic artery is delivered to the lobule at its periphery and flows thence from all sides toward the center, where it enters the

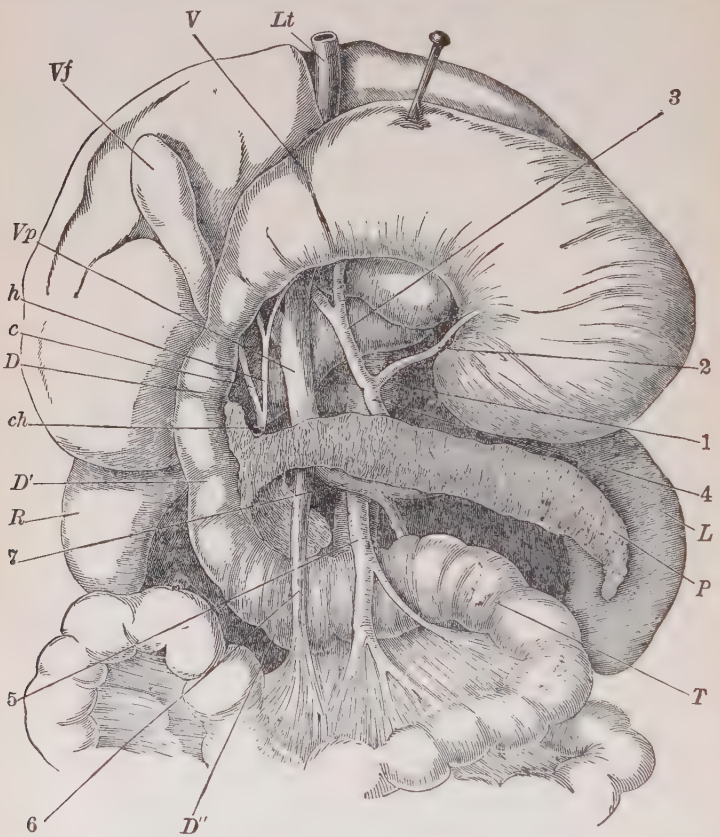


FIG. 139.—The stomach, pancreas, liver, and duodenum, with part of the rest of the small intestine and the mesentery; the stomach and liver have been turned up so as to expose the pancreas. *V*, stomach; *D*, *D'*, *D''*, duodenum; *L*, spleen; *P*, pancreas; *R*, right kidney; *T*, jejunum; *Vf*, gall-bladder; *h*, hepatic duct; *c*, cystic duct; *ch*, common bile-duct; 1, aorta; 2, an artery (left coronary) of the stomach; 3, hepatic artery; 4, splenic artery; 5, superior mesenteric artery; 6, superior mesenteric vein; 7, splenic vein; *Vp*, portal vein.

interlobular vein and is conveyed away. The bile, on the other hand, is secreted by the liver-cells and from them passed into the bile-capillaries; it flows along these toward the periphery where it enters small bile-ducts, and so is carried toward the great outlet of

the gland, the hepatic duct. Within the blood-capillaries of the liver are vast numbers of reticulo-endothelial cells (p. 318), so disposed that they can take up floating particles from the blood-stream.

The Pancreas or Sweetbread. This is an elongated soft organ of a pinkish-yellow color, lying along the great curvature of the stomach. Its right end is the larger, and is embraced by the duodenum (Fig. 139), which there makes a curve to the left. A duct traverses the gland and joins the common bile-duct close to its intestinal opening. The pancreas produces a watery looking secretion which is of great importance in digestion; the gland also secretes a hormone which exerts an important influence on the general nutritional processes of the Body (Chap. XXX).

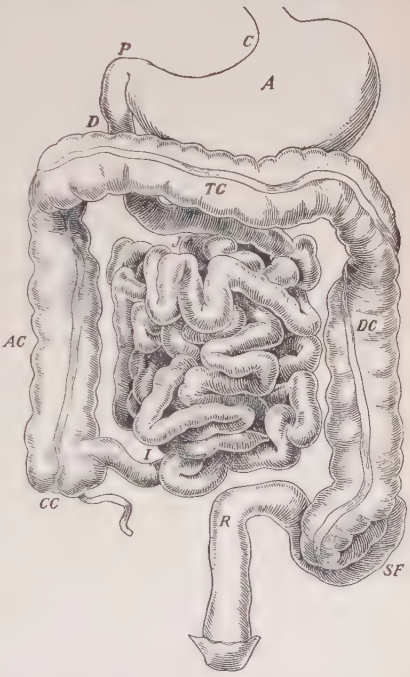


FIG. 140.—Diagram of abdominal part of alimentary canal. *C*, the cardiac, and *P*, the pyloric end of the stomach. *A; D*, the duodenum; *J, I*, the convolutions of the small intestine; *CC*, the cæcum with the vermiform appendix; *AC*, ascending, *TC*, transverse, and *DC*, descending colon; *SF*, sigmoid flexure; *R*, the rectum.

The Blood Vessels of Alimentary Canal, Liver, Spleen, and Pancreas. The portal vein (*Vp*, Fig. 139) has already been referred to as differing from all other veins in that it not only receives blood from a system of capillaries but ends in a second set of capillaries, which lie in the liver. The stomach, the intestines, the liver, the pancreas, and the spleen are supplied with arterial blood from three great branches of the aorta. The most anterior of these, the *celiac axis*, springs from the aorta close beneath the diaphragm and divides into the *hepatic artery*, *splenic artery*, and arteries for the stomach; some of these divisions may be seen in Fig. 139

The pancreas is supplied partly from the hepatic, partly from the splenic artery. The two other branches (*superior* and *inferior mesenteric artery*) are given off from the aorta lower down in the abdominal cavity; the former (5, Fig. 139) supplies the small intestine and half of the large, the latter the remainder of the large. The blood passing through all these arteries becomes venous in the capillaries of the organs they supply, and is gathered into corresponding veins (Fig. 139) which unite near the liver to form the portal vein. The further course of the blood carried to the liver (partly arterial from the hepatic artery, partly venous from the portal system) has been described already (p. 351).

CHAPTER XXVII

THE CHEMISTRY OF DIGESTION

The Object of Digestion is twofold: to prepare the various foods for absorption by the lining of the digestive tract, which means that they must be made soluble if not already so; and to convert them into forms in which the Body can make use of them after they have been absorbed. Digestion is confined to the nutrients; the inorganic salts of the food are soluble, and are used by the Body in essentially the same form as eaten, they therefore need no digestion. The accessories either perform their function in connection with the process of digestion itself, or are absorbed and used by the Body in the form in which they are taken.

Nature of the Digestive Process. Although the foods requiring digestion are of very different sorts chemically, the method of digestion is at bottom the same for all of them. It consists of the process known in chemistry as *hydrolysis*. Hydrolysis is a chemical reaction in which one molecule of the substance involved combines with one molecule of water and the resulting compound splits into two simpler molecules. By repeated hydrolyses very complex substances may be split into comparatively simple ones.

Hydrolysis is a common reaction of organic chemistry. It is probable that it is among the most frequently occurring reactions of the living Body. Not only the digestive processes, but many of the activities of living cells are of this nature. The digestive hydrolyses are all carried on through the agency of *enzyms* (p. 26). There is a special and specific enzym for each particular reaction; the enzym that splits starch is without effect or protein or fat. These enzym reactions are all simple chemical reactions; they are carried on in the alimentary tract as in a chemical laboratory, and will go on just as well in test-tubes kept at Body temperature as in the Body itself. They are not therefore "vital" processes in the sense that they cannot occur except in the presence of living cells.

Digestion Products. Before beginning a detailed description of the digestive process as it affects the different food stuffs it will perhaps be helpful to call attention to the comparatively few

and simple substances which are finally produced as the result of the numerous reactions that go on in the alimentary tract. All carbohydrates (except the single sugars), the starches, gums, and double sugars, are hydrolyzed into *single sugars* during their digestion, so that absorption of carbohydrates is altogether in the form of single sugars. All fats are split into *fatty acid* and *glycerol*, in which state they are ready to be taken up by the intestinal walls. The proteins, as we saw in Chap. I, are complexes built up of a large number of amino acids. The digestive process splits them into simpler molecules each of which is composed either of a single amino acid, or of two or three of them together. We may say, in general, that proteins are split into their constituent *amino acids*.

Tabulating the digestion products we have:

from carbohydrates, single sugars;
from fats, fatty acid and glycerol;
from proteins, amino acids.

The Saliva. The first digestive fluid that the food meets with is the saliva, which, as found in the mouth, is a mixture of pure saliva, formed in parotid, submaxillary, and sublingual glands, with the mucus secreted by small glands of the buccal mucous membrane. This *mixed saliva* is a colorless, cloudy, feebly alkaline liquid, "ropy" from the mucin present in it, and usually containing air-bubbles. Pure saliva, as obtained by putting a fine tube in the duct of one of the salivary glands, is more fluid and contains no imprisoned air.

The uses of the saliva are in part physical and mechanical. It keeps the mouth moist and allows us to speak with comfort; it also dissolves such bodies as salt, and sugar, when they are taken into the mouth in solid form, and enables us to taste them; undissolved substances are not tasted, a fact which anyone can verify for himself by wiping his tongue dry and placing a fragment of sugar upon it. No sweetness will be felt until a little moisture has exuded and dissolved part of the sugar.

In addition to such actions the saliva exerts a chemical one on an important food stuff. It contains an enzym, *salivary diastase*, or *ptyalin*, which has the power of turning starch into a double sugar, *maltose*. This change, like all digestive reactions, is a hydrolysis. It does not occur in a single stage; that is, the starch molecule is

not split directly into maltose, but first into a dextrin which is hydrolyzed into a simpler dextrin, and this in turn into maltose. In effecting the change the diastase is not altered; a very small amount of it can convert a vast amount of starch, and does not seem to have its activity impaired in the process.

In order that the diastase may act upon starch certain conditions are essential. Water must be present, and the liquid must be neutral or feebly alkaline; acids retard, or if stronger, entirely stop the process. The change takes place most quickly at about the temperature of the Human Body, and is greatly checked by cold. Boiling the saliva destroys its enzym and renders it quite incapable of converting starch. Cooked starch is changed more rapidly and completely than raw.

It will be noted that salivary digestion is only a stage in the preparation of starch for the use of the Body, since starch, in common with the other carbohydrates taken as food, is finally converted to single sugar before it is absorbed.

The Gastric Juice. The food having entered the stomach is subjected to the action of the gastric juice, which is a thin, colorless or pale yellow liquid, of a strongly acid reaction. It contains as specific elements *free hydrochloric acid* (about 0.2 per cent), and an enzym called *pepsin* which, in acid liquids, has the power of converting the ordinary proteins which we eat, by hydrolysis, into closely allied bodies, *proteoses* and *peptones*.

In neutral or alkaline media the pepsin is inactive; and cold checks its activity. Boiling destroys it. In addition to pepsin, gastric juice contains another enzym (*rennin*) which coagulates the casein of milk, as illustrated by the use of "rennet," prepared from the mucous membrane of the calf's digestive stomach, in cheese-making (see also p. 461). The curdled condition of the milk regurgitated by infants is, therefore, not any sign of a disordered state of the stomach, as nurses sometimes suppose. It is proper for milk to undergo this change, before the pepsin and acid of the gastric juice digest it.

The Pancreatic Juice. In the intestine the food is subjected to the action of the pancreatic juice. This is clear, watery, alkaline, and much like saliva in appearance. The Germans call the pancreas the "abdominal salivary gland." In digestive properties, however, the pancreatic secretion is far more important

than the saliva, or even the gastric juice. It contains three digestive enzyms; *pancreatic diastase*, or *amylopsin*, a starch-splitting enzym whose action is identical with that of salivary diastase, and which is thought to be, perhaps, itself identical with the latter; *lipase*, a fat-splitting enzym, converting fats to fatty acid and glycerol; *trypsin*, a protein-splitting (*proteolytic*) enzym whose action is much more effective than that of pepsin, as it is able to carry the process of protein hydrolysis clear to the amino-acid stage. It acts upon such proteins as escape the influence of pepsin in the stomach, and also continues the digestion of the proteoses and peptones formed by pepsin action. A noteworthy feature of trypsin action is that it does not apply to all the bonds by which amino acids are held together in the protein molecule; certain of them resist the action of trypsin, and remain unbroken even after prolonged exposure to it.

The Bile. This fluid, which is poured into the intestine from the liver, does not contain any digestive enzym, but it does have an important rôle in connection with fat digestion; it has been shown that pancreatic lipase splits fats several times as rapidly when bile is present as when it is absent.

The Succus Entericus (Intestinal juice). This fluid, which is secreted by the minute glands of the intestinal wall, is the last of the digestive fluids to come in contact with the food, and by its enzyms the carbohydrates, which are not fully digested by the earlier juices, must be finally prepared for absorption. Furthermore, the amino-acid linkages that resist the action of trypsin are to be broken by an enzym of the intestinal juice, in order that protein digestion may be finished. Fats are the only foods which do not require the aid of the succus entericus for their complete digestion.

The digestive enzyms of the succus entericus are four; one proteolytic, *erepsin*, which acts on the amino-acid linkages trypsin fails to break, thus completing the work of the other proteolytic enzyms; and three so-called *inverting* enzyms, which change double sugars to single sugars. These enzyms are specific in their action, each affecting only its particular sugar. *Maltase* inverts maltose, thus completing the starch digestion begun by salivary and pancreatic diastase; *sucrase* splits cane-sugar or sucrose, and *lactase* converts milk-sugar, lactose, to single sugar. The result of the

action of these three enzyms is to bring all the carbohydrates of the food, except cellulose, into the condition of single sugars, in which form they are ready for the use of the Body.

Summary of the Digestive Process. The chemical reactions by which the various food stuffs are made ready for absorption and use by the Body can be conveniently summarized in tabular form:

Region	Secretion	Enzyms	Substances Affected	Products Formed
Mouth	Saliva	Diastase	Starch	Maltose *
Stomach	Gastric Juice	Pepsin	Protein	Proteoses * Peptones *
Small Intestine	Pancreatic Juice	Diastase	Starch	Maltose *
		Lipase	Fats	Fatty acid † Glycerol †
		Trypsin	Proteins Proteoses Peptones	Amino Acids †
	Succus Entericus	Erepsin	Proteins Proteoses Peptones	" "
		Maltase	Maltose	Single Sugar †
		Sucrase	Cane-Sugar	" "
		Lactase	Milk-Sugar	" "

* Intermediate products.
† Final products.

Bacterial Digestion. The human intestines normally contain enormous numbers of bacteria. In the upper and middle parts of the small intestine the action of these is for the most part *fermentation* of carbohydrates with the production of carbon dioxid, alcohol, and lactic acid. There is no doubt that even in perfect health a considerable fermentation goes on in the intestine. So far as appears it is neither particularly harmful nor beneficial. The fermentation products are probably absorbed and used by the Body, but they would be used equally well if absorbed as sugar without fermentation. In the case of one particular carbohydrate,

however, *cellulose*, bacterial fermentation affords the only means by which it can be made available in man for the use of the Body. It seems to be well established that tender cellulose, such as is eaten in lettuce, for example, may be digested by bacteria to a considerable extent; where it is less tender, as in most fruits and vegetables, it remains, as stated earlier, practically undigested in man.

Intestinal fermentation is not essential to health as is shown by the possibility of living normally in arctic regions, where, it is said, intestinal bacteria are sometimes wholly wanting. When the fermentation becomes excessive intestinal disturbances may readily result. The production of fermentation acids in too great concentration leads to irritation of the intestinal wall and causes diarrhea.

In the lower end of the small intestine and in the large intestine the bacterial action is chiefly putrefaction of proteins, rather than fermentation of carbohydrates. The difference is not due to the presence of different species of bacteria, but to the different nature of the available food. Where carbohydrate is present in excess, as in the upper and middle small intestine, fermentation is the normal action. By the time the intestinal contents reach the lower intestine the digestible carbohydrates are, as we shall learn (p. 531), all absorbed out into the blood. There remains, however, a portion of the protein, including all indigestible meat fragments. In this environment, largely protein, the normal bacterial action is of the nature of putrefaction. The characteristic features of the contents of the large intestine are the results of this putrefaction. In connection with it various toxic substances are formed which may be absorbed from the intestine into the blood. The symptoms of heaviness and general ill-feeling that frequently accompany sluggishness of the large intestine have been referred to the presence of these toxins in the blood. The condition is known as autointoxication. To what extent the symptoms of ordinary constipation are due to autointoxication is debatable, as is pointed out later (p. 506).

The Prevention of Self-Digestion. A question of much interest to physiologists has been why the stomach and intestinal walls and the gastric and pancreatic glands are not themselves digested by the powerful proteolytic enzyms which the glands

produce, and which are poured out into the walls of the digestive organs. It has been shown that the prevention of self-digestion of stomach and intestine depends upon the continuance of life, for animals killed in the midst of digesting a meal often do digest great parts of their stomach and intestinal walls. Just how self-digestion of these structures is normally prevented is not clear, except in so far as the mechanism to be described presently (Chap. XXIX), which limits the outpouring of the secretions to periods when food is present, may be efficacious. The self-digestion of the pancreatic and gastric glands is, however, prevented by an interesting arrangement which has been recently analyzed. It appears that neither pepsin nor trypsin is formed in the gland as an active enzym but in an inactive *pro-enzym* or *zymogen* form, *pepsinogen* or *trypsinogen*, which becomes active only when converted into pepsin or trypsin by some activating agent. It has been shown that the conversion of pepsinogen to pepsin is due to the action of the hydrochloric acid of the gastric juice; while that of trypsinogen to trypsin occurs when the pancreatic juice is poured into the small intestine, and is brought about through a constituent of the succus entericus, *enterokinase*. This substance is believed to be an enzym having the sole function of activating trypsinogen to trypsin.

CHAPTER XXVIII

MOVEMENTS OF THE ALIMENTARY CANAL

Mastication serves to break the food into fine particles and by mixing it intimately with saliva to reduce it to a semiliquid state. It consists primarily of cutting and grinding the food between the upper and lower teeth, a process which is performed by movements of the lower jaw. The articulation of the lower jaw with the skull and its equipment of muscles permit both up and down cutting movements and sidewise grinding movements. The actual chewing process involves, in addition, motions of the lips, cheeks, and tongue in holding the food in position for the teeth to act upon it. The whole process is performed by skeletal muscles and is, therefore, under the control of the will, although actually carried on, for the most part, as a conditioned reflex (p. 173); the sensory stimuli are partly of mechanical and partly of chemical origin, evoked by the presence of substances in the mouth.

It ought not to be necessary to emphasize the importance of thorough mastication of the food. Salivary digestion depends wholly, of course, upon the bringing of saliva into contact with the starch particles, and it can easily be shown experimentally that gastric digestion is several times more rapid when the material exposed to the action of gastric juice is finely divided than when it is in large masses.

The interesting fact has recently been brought out that the more the process of masticating each mouthful is prolonged the less food is required to satisfy the appetite. Since many people doubtless eat too much there is here a suggestion as to a way of reducing the amount taken without serious sacrifice of enjoyment of the food.

Hygiene of the Mouth. The mouth cavity is almost never free from micro-organisms. The slightly alkaline reaction of saliva is favorable to their growth, and they scarcely ever lack for food. The irregularly shaped teeth, packed closely along the jaw, have between them spaces where material that is being chewed readily

lodges, and where it stays unless special care is taken to remove it. Such lodged food-masses shortly harbor flourishing colonies of bacteria. These in connection with their growth and multiplication produce substances which attack the protective enamel of the teeth and so gain foothold within the tooth substance itself, and we have under way the too-familiar process of tooth decay. Good teeth are so important for efficient mastication, as well as for the appearance of the face, that no pains should be spared to preserve them. Evidently the way to do this is to prevent the accumulation of bacteria in the spaces between them. Thorough cleaning, desirably after each meal, with the occasional use of an antiseptic mouth-wash is fairly but not completely satisfactory. Half-yearly inspection and cleaning by a dentist are usually necessary to supplement one's own efforts, because of the practical impossibility of keeping every one of the small mouth spaces clear. Such inspection also insures the discovery of decay while the cavities are still small, and makes possible the preservation of the teeth in approximately normal condition for many years.

Recently evidence has been advanced showing that the saliva varies slightly in alkalinity in different people, and that the susceptibility of the teeth to decay depends largely on the degree of alkalinity. Three general groupings are suggested. Those who fall within the limits of the first group are likely to have perfect teeth even though no care is taken of them. The second group can have good teeth by the exercise of reasonable care. The third group have difficulty in preserving the teeth in good condition in spite of unremitting attention to them. This observation explains the frequent occurrence of perfect teeth in savages and others who never pay them the slightest attention, and the prevalence of decay among the most highly civilized. It is probable, although not proven, that the nature of the diet has much to do with the degree of alkalinity of the saliva.

Of late years a great deal of attention has been paid to indirect harm that may follow neglect of the teeth. Allowing colonies of bacteria to flourish undisturbed at their roots means, of course that any toxins these may produce will be absorbed into the system. The result of continuous absorption of such toxins is often manifested in lowering of the general health. Specifically, acute rheumatism is said frequently to follow.

Deglutition. A mouthful of solid food is broken up by the teeth, and rolled about the mouth by the tongue, until it is thoroughly mixed with saliva and made into a soft pasty mass. This mass is sent on from the mouth to the stomach by the process of *deglutition* or swallowing, which is described as occurring in three stages. The first stage includes the passage from the mouth into the pharynx. The food being collected into a heap on the tongue, the tip of that organ is placed against the front of the hard palate, and then the rest of the tongue is raised from before back, so as to press the food-mass between it and the palate, and drive it back through the fauces. This portion of the act of swallowing is voluntary, or at least is under the control of the will, although it commonly occurs reflexly. The second stage of deglutition takes place rapidly, not requiring more than a second, and thus emptying the pharynx quickly so as to clear the opening of the air-passages for breathing purposes. The food-mass, passing back over the roof of the tongue, pushes down the epiglottis; at the same time the larynx (or voice-box at the top of the windpipe) is raised, so as to meet it, and thus the passage to the lungs is closed; muscles around the aperture probably also contract and narrow the opening. The raising of the larynx can be readily felt by placing the finger on the large cartilage forming "Adam's apple" in the neck, and then swallowing something. The soft palate is at the same time raised and stretched horizontally across the pharynx, thus cutting off communication with its upper, or respiratory portion, leading to the nostrils and Eustachian tubes. Finally, the isthmus of the fauces is closed as soon as the food has passed through, by the contraction of the muscles on its sides and the elevation of the root of the tongue. All passages out of the pharynx except the gullet are thus blocked, and by a sharp contraction of the mylohyoid muscles, in the floor of the mouth, such great pressure is put upon the food-mass as to shoot it clear through the pharynx into the opening of the esophagus. Liquids or very soft foods, under the impetus given by the contraction of these muscles, are propelled the whole length of the gullet to the sphincter which guards the entrance to the stomach; more solid masses are thrown only into the entrance of the gullet whence the third stage of swallowing conveys them to the stomach. The muscular movements concerned in this part of deglutition are all reflexly excited; food

coming in contact with the mucous membrane of the pharynx stimulates afferent nerve-fibers in it; these excite efferent nerve-fibers proceeding to the muscles concerned and cause them to contract in proper sequence. The pharyngeal muscles, although of the striped variety, are but little under the control of the will; it is extremely difficult to go through the movements of swallowing without something (if only a little saliva) to swallow and thus excite the movements reflexly. Many persons, after having got the mouth completely empty cannot perform the movements of the second stage of deglutition at all. On account of the reflex nature of the contractions of the pharynx, any food which has once entered it must be swallowed: the isthmus of the fauces is a sort of Rubicon; food that has passed it must continue its course to the stomach, although the swallower learnt immediately that he was taking poison. The third stage of deglutiton is that by which solid food is passed along the gullet, and is comparatively slow. The movements of the esophagus are of the kind known as *peristaltic*. Its circular muscular fibers contract behind the morsel and narrow the passage there; and the constriction then travels along to the stomach, pushing the food in front of it. Simultaneously the longitudinal fibers, at the point where the food-mass is at any moment and immediately in front of it, relax, tending to widen the passage. This peristaltic wave requires about six seconds in man for its passage along the esophagus. It is part of the reflex act of swallowing and takes place whenever the act occurs, whether there be any food-mass to be conveyed to the stomach or not. The ring of smooth muscle of the circular coat at the entrance of the stomach acts as a sphincter (cardiac sphincter). This is ordinarily tightly contracted when there is food in the stomach, holding the esophagus shut, and only opens at the approach of the peristaltic wave to allow the food-mass to pass through into the stomach. Liquids, which pass very quickly down the esophagus (in 0.1 sec.), usually do not get into the stomach at once, but are held by the sphincter until the arrival of the peristaltic wave opens a passage for them. The relaxation of the cardiac sphincter under these circumstances does not open a free communication between the stomach and the throat for there is always a descending peristaltic wave holding the esophagus closed. This is important because, as we shall see, the

stomach contents are under pressure, and would be forced up into the esophagus were the sphincter to relax with no peristaltic wave present. As a matter of fact this sometimes happens, particularly in persons suffering from indigestion, or certain nervous disorders, or in users of tobacco. The upward rush of the acid stomach contents into the esophagus gives rise to a burning sensation which is generally known as "heartburn," although the heart has really nothing whatever to do with it.

Movements of the Stomach. When the stomach is first emptied of food its condition for a time is usually that of a flabby pouch, with walls neither much relaxed nor greatly distended. There are probably always a small amount of liquid (gastric juice and saliva) and some bubbles of swallowed air in the stomach, even when we speak of it as empty. The flabby condition usually does not persist long; presently the circular muscle coat of the stomach goes into a state of tonus, the effect of which is to contract the organ until it is little more than a tube, slightly enlarged at the fundic end. Shortly before the usual time for taking a meal a flow of impulses over the vagus nerves begins, accentuating the tonus, and giving rise to the active "hunger contractions" (p. 225). As food is swallowed and enters the nearly tubular stomach the walls relax their tonus sufficiently so that their pressure on the stomach contents is not increased. In other words, the entry of food into the stomach does not put its walls on the stretch. This adjustment continues until the normal capacity of the organ is reached; if engorgement continues beyond that point actual stretching occurs, with ultimate damage to the structures concerned. One result of this manner of filling the stomach is that the food is deposited in it in layers, the first food taken being next to the walls, subsequent amounts being toward the center, and the further from the walls the more has entered before them.

The acid-secreting gastric glands (p. 477) are confined to the middle and prepyloric portions of the stomach. Food in the fundus is not, therefore, very quickly acidified. The action of salivary diastase, which is brought to an end when the food becomes acid, may thus continue in the fundic region for a considerable time after the food is swallowed, especially in those portions of food which are swallowed late in the meal.

The movements of the stomach have been watched by means

of the X-rays. Food which has been mixed with bismuth subnitrate is opaque to these rays and its movements in response to the movements of the stomach walls can be readily followed. By this means it has been learned that the walls of the stomach show peristaltic waves; these begin at about the middle, in a strong contraction of a ring of circular muscles at that point, and sweep to the pylorus. The fundic end is not involved at all in them. In man they recur regularly, so long as food is in the stomach, at intervals of about 2½–3 seconds. Individual waves take about 10 seconds to pass from their point of origin to where they die out at the pyloric sphincter. Consequently three or four waves are usually present simultaneously in the stomach. For a considerable period after food enters the stomach the *pyloric sphincter*, which guards the exit into the small intestine, remains perfectly tight. During this time the peristaltic waves crowd the food caught by them up to the pylorus but cannot force any through. As the constriction approaches the pylorus the food-mass in front of it escapes back through the opening at its center, the waves not being deep enough to close this entirely, and so the food in the central and pyloric portions of the stomach is thoroughly churned.

During this churning the food, already semiliquid from the mixture with saliva and with such liquid as was taken with the meal, is mixed with the gastric juice and made still more liquid, being called at this stage *chyme*. The effect of the gastric juice is to give the food an acid reaction, stopping the action of ptyalin and permitting that of the pepsin which it also pours out upon the food.

The Control of the Pyloric Sphincter. The way in which the sphincter of the pylorus is regulated so that after the food has been thoroughly mixed with gastric juice it opens and allows a small amount to pass to the intestine, and then promptly closes to give opportunity for this to be influenced by the intestinal secretions before more is admitted, is one of the most interesting adaptations that we know of in the Body. The mechanism of this action is a special case of a peculiar reflex which apparently obtains through much of the alimentary canal, although absent from all the stomach except the pyloric sphincter, and from the large intestine, and is probably dependent on special properties of the nerve plexus which is imbedded therein. This so-called *myenteric reflex*, is of such a

sort that a stimulus applied to any point along the alimentary canal causes a contraction of the muscles immediately in front of (anterior to) the stimulated point, and a relaxation of those immediately behind (posterior to) it. The reflex was worked out first for the small intestine, and has since been shown to apply to some other parts of the canal. It is a so-called "local reflex," as the central nervous system has nothing whatever to do with it.

One adequate stimulus for arousing the reflex in the pyloric sphincter, although probably not the only one, is the presence of free acid. When therefore the originally alkaline food in the pyloric part of the stomach has been completely neutralized by the acid of the gastric juice, and excess acid begins to accumulate, the pyloric sphincter is stimulated, but from the stomach side, and according to the working of the myenteric reflex a stimulus from that side produces relaxation of a region just posterior to it. As soon as the sphincter relaxes under this stimulation part of the food lying in the pylorus is forced through into the intestine, but it carries with it the free acid with which the food is mixed and stimulates the sphincter from the intestinal side, namely, from behind, and therefore tends to cause it to close. A feature of the myenteric reflex is that where, as just described, a point is simultaneously stimulated from in front and from behind, the stimulus causing contraction, that from behind, is dominant. Therefore as soon as food enters the intestine the sphincter of the pylorus contracts and prevents more from passing. Before it will relax again the acid on its intestinal side must be neutralized; but this is rapidly done by the strongly alkaline bile and pancreatic juice, and so as fast as the food in the intestine is mixed with these juices more is admitted from the stomach. X-ray studies in man indicate that mechanical stimulation (pressure of the food mass as a wave crowds it against the sphincter) may also be effective in opening the sphincter. This implies a back pressure to close it again after some chyme passes through. The details of this back pressure, and how it is relieved to allow the sphincter to open again, have not been worked out.

The fundus of the stomach, which stores the bulk of the food while that in the pylorus is being thus treated and passed on to the intestine, is pressing on the stomach contents all the time, so that as fast as food is passed out through the pyloric sphincter

more is pushed to the pylorus from the fundus until at last the stomach is wholly emptied. The time required for emptying the stomach completely varies with different foods and under different bodily conditions. An average meal is probably all out of the stomach about four to six hours after eating.

An interesting incidental feature of this mechanism is that it operates automatically to pass quickly on into the small intestine carbohydrate food stuffs, which undergo no digestive action in the stomach, while proteins, upon which the pepsin of gastric juice acts, remain long enough to ensure their thorough mixture with the juice. This differentiation depends on the fact that the acid does not enter any chemical combination with carbohydrates, and therefore begins to appear in excess as soon as the alkali present has been neutralized. Proteins, on the other hand, do combine chemically with the acid, and there can be no excess, therefore, until this combination has occurred. Meanwhile thorough mixture with pepsin is taking place. This difference does not show, of course, in the case of a mixed meal, but a meal of pure carbohydrates will begin to leave the stomach much sooner after ingestion than a meal of pure protein (10–15 minutes as compared with ½ hour), and will be discharged completely in half the time (2–2½ hours as against 4–5); and a meal in which the carbohydrates are eaten before the proteins may show a definite interval between the discharge of the last carbohydrates and the first proteins. The admixture of fats with the other food stuffs delays considerably the rate of discharge.

The pyloric sphincter does not hold against pure water nor against substances of the consistency of raw egg-white or raw oysters. These, unless mixed with other materials, pass promptly, therefore, from the stomach into the small intestine.

Importance of the Stomach. Aside from its function of beginning the digestion of proteins, a function which, as we have seen (p. 492) is subordinate to the more efficient digestive action of the small intestine, the chief significance of the stomach is that it enables us to take our daily supply of food in three meals, more or less, according to our habit. The small intestine is a narrow tube. The ducts of pancreas and liver open into its upper end. If our food when swallowed passed directly into the intestine each mouthful would crowd the preceding ones along at such a rate that no ade-

quate admixture with the essential juices of the pancreas and liver could occur, and very little digestion would take place. To avoid this difficulty the food would have to be eaten little by little, and to get enough for the needs of the Body would require hours of steady nibbling. By affording storage to a considerable amount of food, which is automatically passed along to the intestine at just the rate at which that region can handle it, the stomach permits us to follow eating habits much less time-consuming, and more convenient.

Movements of the Small Intestine. The food entering the small intestine is subjected to two sorts of movements whose combined effect is to churn it very thoroughly and to move it slowly along the gut so as to make room for more to come in from the stomach. The churning is effected mainly by movements of the intestine known as *rhythmic segmentation.* In these movements rings of the circular muscle coat about an inch apart constrict simultaneously, splitting the contained food into a series of segments; an instant later these constrictions disappear, and new ones, midway between the first, are formed, by which the food is again segmented, but in a shifted position. The third set occupy the same position as the first, the fourth as the second, and so on. These rhythmic movements may recur as often as twenty times a minute in the duodenum and upper jejunum, only about half as frequently in the lower jejunum and ileum. Their effect is to bring every particle of the contained food into intimate contact with the intestinal walls, insuring thorough mixing with the intestinal secretions, and also favoring absorption.

The onward movement of the food is secured by *peristaltic waves* which start at the pylorus and run rather slowly along the intestine propelling the chyme ahead of them. During digestion the two sorts of movements alternate more or less irregularly. After the segmentation has churned a food-mass thoroughly in one section it dies away and a peristaltic wave develops, which carries the food ahead of it into a fresh section; then the peristalsis, in turn, subsides, and segmentation is resumed.

The mechanism of these intestinal movements is not entirely clear, the peristaltic waves, and possibly also the segmentations, are special manifestations of the myenteric reflex described above, but the conditions that govern their appearance and disappear-

ance, first in one part of the intestine and then in another, are not known.

Observations with the X-rays have shown that the rate of progress of the food through the human small intestine is about 4½ feet in the hour, so that the first food from any meal may appear at the ileocolic valve about 4½ hours after it begins to leave the stomach.

Extrinsic Control of Stomach and Intestinal Movements. It has been shown that normal movements of both stomach and intestine may go on in animals in which the nerves leading to these organs from the central nervous system are cut. To a certain extent, therefore, they, like the heart, contain within themselves the essential requirements for normal activity. Like the heart, however, they are subject to reflex control through the central nervous system.

The vagus nerves carry cranial autonomic fibers which when stimulated arouse the stomach and intestine to activity. The opposing thoracico-lumbar autonomics, which, as we have already seen (p. 396), come by way of the splanchnics, are inhibitory. A part of the *emergency reaction* of the Body, therefore, consists in suspension of activity in these organs. This has been noted previously (p. 209).

Movements of the Large Intestine. During the passage of the food through the small intestine the greater part of its nutritive content is absorbed, but practically none of the water, so that it is delivered through the ileocolic valve to the large intestine in a very watery condition. The parts of the large intestine next to the small intestine, the ascending and transverse colon, show an interesting movement in the form of an *antiperistalsis*. This is a peristaltic wave which begins in the transverse colon and sweeps toward the ileocolic valve. It would tend to force the material within the colon back into the small intestine did not the ileocolic valve prevent. The result of this movement is a churning and mixing of the contents whereby the absorption of the last useful materials, including the water, is promoted. As the large intestine is filled more and more from the small, some of its contents are crowded, in spite of the antiperistalsis, into the far end of the transverse colon, where regular peristaltic waves carry them on through the descending colon to the sigmoid flexure and the rectum, whence they are discharged from the Body. There is evidence that

the stimulus for these intestinal waves is mechanical, depending on stretching of the walls by the intestinal contents.

Importance of Roughage. As the result of the absorption of water from the contents of the large intestine the material remaining, which consists of undigested substances, bacteria, the products of bacterial action, and some waste products excreted in the bile (p. 550), tends to become dry and closely packed. If the diet is poor in roughage (p. 453) so little room is occupied by this material that the necessary mechanical stimulation fails to be forthcoming for the movements by which it should be carried along to the region of discharge. There is, therefore, stagnation in the large intestine, and this, by permitting time for a more complete absorption of water, makes the condition of affairs still worse, and the evacuation of the colon still more difficult. The inclusion of considerable roughage in the diet (bran, the pulp of vegetables and fruits, particularly apples, popcorn) by increasing the bulk of the intestinal contents favors the onward movement of the material, and tends against stagnation. We need to remember in this connection that the colon is a smooth muscle structure, under the control of the autonomic system, and subject, therefore, to the disturbing influences characteristic of such structures. The inclusion of ample roughage in the diet does not always suffice to secure adequate evacuations, particularly where neglect or improper treatment has affected the colon so that it no longer responds normally to mechanical stimulation from its contents. The means commonly used to induce evacuations, the taking of purgative drugs, is objectionable, although sometimes necessary, because the drugs act by irritating the intestinal lining. Such irritation, if repeated regularly, brings on a chronic inflammation, which seriously impairs the ability of the colon to react normally. The habit of taking purgative drugs should be strenuously avoided. If persisted in it is sure to lead to much discomfort or even severe suffering. It is probable that much of the trouble from intestinal sluggishness could be avoided by proper supervision and care in childhood, when regular habits are easy to establish and enforce. Regularity, even more than ample roughage, is a prime requisite to the proper functioning of the colon.

Cause of Constipation Symptoms. When fecal material is retained overlong in the rectum definite symptoms, usually

known as "biliousness," develop. They include mental haziness, headache, loss of appetite, general lowering of efficiency. Although commonly attributed to poisoning of the Body by absorbed products of intestinal putrefaction (autointoxication), it appears that they are more often actually due to nervous and mechanical disturbances set up by the accumulated mass of hard and dry material in the lower bowel. Favoring this idea is the common experience of prompt and marked relief following evacuation of the bowels; the relief coming on much quicker than poisons could be got rid of. Of course true autointoxication does occur, but as often in diarrhea as in constipation.

CHAPTER XXIX

THE DIGESTIVE SECRETIONS AND THEIR CONTROL

Organs of Secretion. The simplest form in which a secreting organ occurs (*A*, Fig. 141) is that of a flat membrane provided with a layer of cells, *a*, on one side (that on which the secretion is poured out) and with a network of capillary blood vessels, *c*, on the other. The dividing membrane, *b*, is known as the *basement membrane* and is usually made up of flat, closely fitting connective-tissue corpuscles; supporting it on its deep side is a layer of connective tissue, *d*, in which the blood vessels and lymphatics are supported. Such simple forms of secreting surfaces are found on the serous membranes, but are not common; in most cases an extended area is required to form the necessary amount of secretion, and if this were attained simply by spreading out plane surfaces, these from their number and extent could not find room in the Body. Accordingly in most cases, the greater area is attained by folding the secreting surface in various ways so that a large area is packed in a small bulk, just as a Chinese lantern when shut up occupies much less space than when extended, although its actual surface remains of the same extent. In a few cases the folding takes the form of protrusions into the cavity of the secreting organ as indicated at *C*, Fig. 141, and found on some synovial membranes; but much more commonly the surface extension is attained in another way, the basement membrane, covered by its epithelium, being pitted in or involuted as at *B*. Such a secreting organ is known as a gland.

Forms of Glands. In some cases the surface involutions are uniform in diameter, or nearly so, throughout (*B*, Fig. 141). Such glands are known as *tubular;* examples are found in the lining coat of the stomach (Fig. 133); also in the skin (Fig. 147), where they form the *sweat-glands*. In other cases the involution swells out at its deeper end and becomes more or less sacculated; (*E*) such glands are *racemose* or *acinous*. The small glands which form the oily matter poured out on the hairs are of this type. In both kinds the lining cells near the deeper end are commonly different in

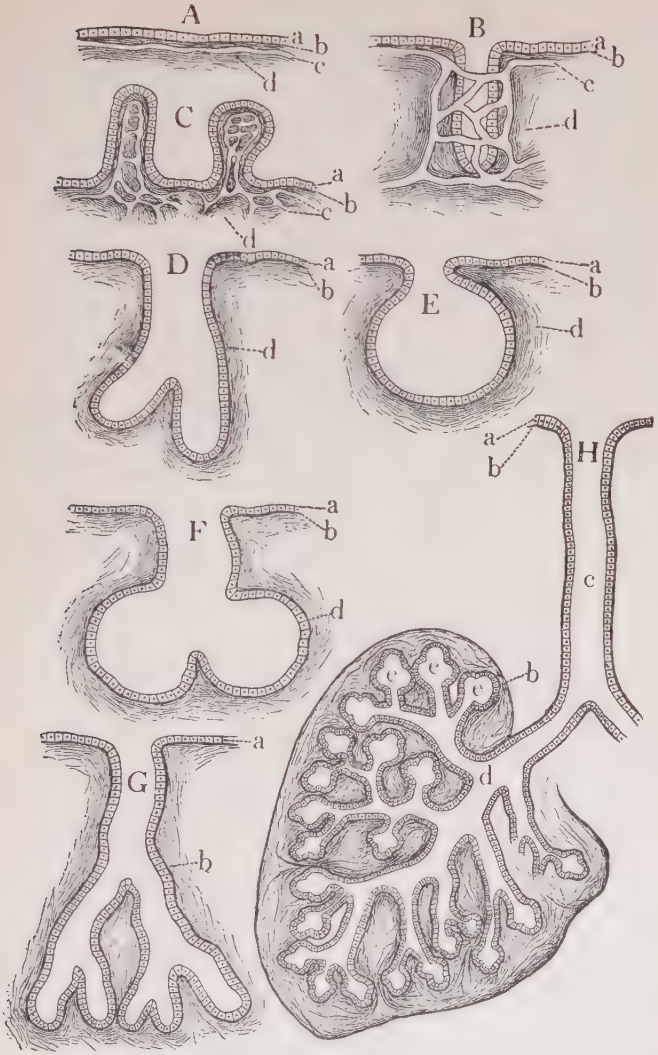


FIG. 141.—Diagrams to indicate forms of glands. *A*, a simple secreting surface; *a*, its epithelium; *b*, basement membrane; *c*, capillaries; *B*, a simple tubular gland; *C*, a secreting surface increased by protrusions; *E*, a simple racemose gland; *D* and *G*, compound tubular glands; *F*, a compound racemose gland. In all but *A*, *B*, and *C* the capillaries are omitted for the sake of clearness. *H*, half of a highly developed racemose gland; *c*, its main duct.

character from the rest; and around that part of the gland the blood vessels form a closer network. These deeper cells form the true secreting elements of the gland, and the passage, lined with different cells, leading from them to the surface, and serving merely to carry off the secretion, is known as the *gland-duct*. When the duct is undivided the gland is *simple;* but when, as is more usual, it is branched and each branch has a true secreting part at its end, we get a compound gland, tubular (*G*) or racemose (*F*, *H*) as the case may be. In such cases the main duct, into which the rest open, is often of considerable length, so that the secretion is poured out at some distance from the main mass of the gland.

A fully formed gland, *H*, thus comes to be a complex structure, consisting primarily of a duct, *c*, ductules, *d*, and secreting recesses, *ee*. The ducts and ductules are lined with epithelium which is merely protective and differs in character from the secreting epithelium which lines the deepest parts. Surrounding each subdivision and binding it to its neighbors is the *gland stroma* formed of connective tissue, a layer of which also commonly envelops the whole gland, as its *capsule*. Usually on looking at the surface of a large gland it is seen to be separated by partitions of its stroma, coarser than the rest, into *lobes*, each of which answers to a main division of the primary duct; and the lobes are often similarly divided into smaller parts or *lobules*. In the connective tissue between the lobes and lobules bloodvessels penetrate, to end in fine capillary vessels around the terminal recesses. They never penetrate the basement membrane. Lymphatics and nerves take a similar course; there is reason to believe that the nerve-fibers penetrate the basement membrane and become directly united with the secreting cells of some glands.

The Secretory Process. The function of glands is to elaborate and pour out a liquid, the *secretion*. It is obvious that the ultimate source of the secretion is the blood circulating through the gland. The digestive secretions, as we have already seen, contain, in addition to water, and inorganic salts, special chemical substances, the *enzyms*, which are different in different glands. It is easy to believe that the water and salts of the gland, since they are precisely the same as occur in blood, may be withdrawn from the blood through physical processes, filtration and dialysis (Chap. II). The special constituents of each secretion, being

different from anything contained in the blood, must, on the other hand, be produced by chemical processes within the gland itself. It is easy to show microscopically that the cells of most glands during rest become filled with small granules, and that when the gland is active these granules for the most part disappear. We can picture the entire secretory process as occurring in two stages: the first, a chemical stage, during which the peculiar constituents of the secretion are elaborated and deposited within the cells of the gland; and a second physical stage consisting of a rapid flow of water with its dissolved salts from the blood through the gland into its duct, carrying with it the special materials previously prepared by the gland.

Nervous Control of the Secretory Process. Considerable evidence has accumulated indicating that gland tissue, like skeletal muscle tissue, carries on its function only when stimulated to do so, and that the stimulus is in many glands nervous. It can easily be shown for the salivary glands of dogs, for example, that proper stimulation of certain nerve-fibers leading to them causes them to pour out their secretion. It is interesting to note that the nerves which cause the gland to pour out its secretion usually cause also vasodilation within it; an increased flow of blood through the gland therefore usually accompanies the physical part of secretion. That this increased blood-flow is not the sole cause of the outpouring of the secretion, as might easily be supposed, is proved by the possibility under proper conditions of stimulating a gland to pour out its fluid without any accompanying vasodilation. We must recognize, then, that the physical act of secretion is the result of the action of definite *secretory* nerves, as distinct from vasodilator nerves.

According to the conception of stimulation given in Chapter II the secretory nerves are thought to act by *increasing the permeability* of the faces of the gland-cells fronting on the *lumen*, or central cavity. As the result of this heightened permeability certain molecules or ions escape, the prevailing equilibrium is upset, and a flow of water and salts takes place, sweeping with it the special enzyms or the mucus which constitute the gland's particular contribution. A feature of this latter action is the conversion, in nearly all glands, of the zymogen or mucigen present in the resting cells into active enzym or fully formed mucin. The conversion

takes place during the act of secretion, except in the one or two cases in which the enzym is secreted in zymogen form, to be activated later (p. 495).

In all glands new formation of the special zymogens or of mucigen takes place spontaneously whenever the quantity present within the cells is lessened by secretion. The process may be said to constitute part of the functional metabolism of glands, in the same sense that recovery oxidation is of muscle-cells (p. 116). But it is important to note that while the outpouring of the secretion is looked on as a physical process, based probably on filtration and dialysis, the force which causes movement of fluid to occur is furnished in large part by metabolic processes within the cells, and is not simply the force of blood-pressure within the capillaries. The proof of this is that saliva, for example, will be secreted with force enough to overcome a back pressure quite definitely greater than the capillary blood-pressure. How this force is brought to bear we do not know, except that the energy displayed is derived from oxidations within the cells. We can revise our picture of gland-cell stimulation, as given above, by saying that when the equilibrium within the cells is disturbed metabolic processes are set off leading to a passage of water and salts from blood to ducts, and incidentally sweeping along the enzyms or mucin. In some of the glands reformation of zymogen takes place rapidly enough to keep pace with the discharge of the same in the secretion. In others the reformation is slower. As we should expect, continued stimulation of the secretory fibers leading to such a gland results soon in the production of a secretion which is very watery, virtually free from the special chemical substances that usually are present in the secretion.

The efferent nerves to glands belong, without exception, to the autonomic system. Glands are, therefore, under reflex control, and not subject to the will.

Hormone Control of Gland Activity. Some of the digestive glands, notably the pancreas, appear to be largely independent of nervous influences. Their control is vested mainly in hormones. The details of this method of control will be described in connection with the glands themselves. It may be noted here, however, that in general those glands whose secretions are needed early in the digestive process are under reflex control, and those whose

secretions may not be required for some time after are under hormone control.

Control of the Salivary Secretion. The salivary glands are subject to reflex stimulation. We must inquire, therefore, what sensory stimuli may excite the reflex. At least three sorts of stimuli are effective to this end: mechanical, the presence of dry substances in the mouth, or merely the rubbing of the tongue against the palate and jaws; chemical, the presence of sapid substances upon the tongue; and psychic, the thought of savory food, as when the mouth "waters." The effects of these different types of stimulation on the character of the saliva differ somewhat; mechanical stimulation arouses reflex excitation chiefly of the parotids, which pour out a much more watery secretion, than do the submaxillaries and sublinguals, which are excited particularly by chemical stimuli, and pour out a thick and viscid saliva. By this difference in the glands excited the character of the saliva is adapted to the nature of the exciting stimulus. The mucous lining of the mouth and throat requires constant moistening. For this a watery saliva is adequate, and such a saliva is poured out whenever the dryness of the mouth becomes pronounced enough to act as a stimulus. When food is taken, on the other hand, the proper functioning of saliva requires that it be rich in diastase. Chemical stimulation, therefore, excites a secretion containing this substance in abundance.

The watering of the mouth at the thought of food is an example of an emotional reflex through the autonomic system such as was discussed earlier (Chap. XII). Inhibition of the salivary glands, leading to dryness of the mouth, as the result of excitation of the thoracico-lumbar autonomic system in time of stress, has also been described.

The Control of the Gastric Secretion. Our present knowledge of the mechanism for controlling the secretion of gastric juice is the result of some of the most interesting investigations of modern Physiology. Many workers have had a share in the solution of the problem but the name of one of them, the Russian physiologist Pavlov (Pávloff), is more closely associated with it than that of any other one man. Pavlov's chief contribution was the demonstration that the increased secretion of gastric juice which occurs when food is eaten is in its early stages excited reflexly, and by

only one particular sort of stimulus, namely, the psychical state accompanying the eating of food which is enjoyed. Pavlov gained this information through feeding experiments on dogs which had been prepared in a special way for the study. The preparation consisted of making a fistulous opening into the stomach, through which the secretion of gastric juice could be followed, and of cutting the esophagus in the neck and bringing the cut ends to the surface in such fashion that all the food swallowed reappeared at the upper esophageal opening, and none reached the stomach unless it was placed within the lower section of the esophagus through its opening. Dogs thus operated upon recovered promptly and completely and could be studied very satisfactorily. It was found that one of these dogs would eat with the greatest enjoyment, although none of the food reached the stomach, and that within a few minutes of the beginning of eating a copious secretion of gastric juice began to be poured into the stomach. That this secretion was excited reflexly was proved by cutting the vagus nerves, after which it never appeared. That it depends upon a certain psychical state, and not upon the mere eating of food was shown in various ways. Dogs which were not hungry would chew and swallow food, but without signs of much interest in it; no secretion was evoked. Meat which had been boiled till it was tasteless was eaten without the production of a secretion. These results make it clear that the stimulus is a psychical one, and that it depends upon active enjoyment of food. Equally important is the observation, made upon these same dogs, that unfavorable emotional states prevent the secretion of the juice. If the dog was angered while eating no juice appeared; even the presence of an attendant for whom he had an aversion sufficed to prevent the secretion. All these facts, established first upon dogs, have been proved true likewise for human beings.

Pavlov's studies showed, moreover, that the "appetite" secretion is not the only secretion of gastric juice which occurs during the digestion of a meal. This was proved by the simple observation that the amount of juice secreted during the eating of a "fictitious meal" is much less than that produced if the food eaten enters the stomach. We must look, then, for some other stimulating agency additional to the psychical one. In such a search the attention turns naturally to the foods swallowed. Do they serve

as chemical stimuli for the production of the additional secretion? It has been shown that some foods, milk and water very slightly, the juices of meat more, do excite the secreting mechanism somewhat, but the really effective excitant appears to be something produced during the process of gastric digestion itself. Thus if the taking of food is attended with pleasure, so that an appetite secretion is produced, the digestive process is started and itself furnishes the stimulating agent for the additional secretion needed to complete the digestion. On the other hand, food eaten during an unfavorable emotional state may fail of digestion completely, through the active suppression of the factors which normally lead to an outpouring of the juice.

Nature of the Supplementary Secretion. Just how these excitants, which presumably act by virtue of their chemical nature, produce their result is not known. Some investigators think that they may irritate the gastric glands directly; others hold the view that they combine with some substance normally present in the lining cells of the pyloric region to form a hormone, which is distributed by way of the blood-stream to the glands. It is true that an acid extract of the pyloric mucosa injected into the blood evokes a secretion of gastric juice, but so does a similar extract of a great variety of animal and plant tissues. This latter fact does not rule out the possibility that a hormone may be formed as described above, but it throws doubt on the theory, compelling us to wait for further evidence before reaching a final decision in the matter.

Contrary to the view held for some years, that gastric juice is secreted only when food is being eaten and digested, it has been shown lately that there is a small continuous secretion, varying from time to time in quantity, but averaging as much as 30 c. c. per hour, or ½ c. c. per minute. Compared with this we have a flow during the height of activity of about 3½ c. c. per minute, a sevenfold augmentation; 700 c. c. or more may be formed during the digestion of a single meal. This continuous secretion is important in that it may take the place of the appetite secretion as a means of getting the process of gastric digestion started, so that even though there be no abundant appetite secretion enough digestion-products may be formed to start the supplementary secretion off, and so bring about the digestion of the entire meal. It should be borne in mind, however, that an

unfavorable emotional state may inhibit the secretion process in toto, a fact which explains the frequent failure of digestion to occur properly when it would seem that the continuous secretion ought to suffice to start it off, even though the appetite secretion has not been aroused.

Control of the Pancreatic Secretion. Proper regulation of the outpouring of pancreatic juice requires that it begin about the time food begins to pass from the stomach into the small intestine. Since this may occur at a variable time after the eating of the meal, it would seem to call for a regulating mechanism quite independent of the act of eating. It has been shown that this requirement is fulfilled through the action of a hormone which is produced in active form during the time that food is passing from the stomach into the small intestine, and only then. The mucous membrane of the small intestine at its upper end contains a substance which has been named *prosecretin*. This substance reacts with hydrochloric acid to form pancreatic *secretin*, the hormone for exciting the pancreas to secrete. But this region of the small intestine comes in contact with hydrochloric acid only at the moment when a mass of food is entering it from the stomach; we have previously seen that this passage of food occurs only when the food is mixed with excess of hydrochloric acid. Thus the production of the hormone is confined to the time when its stimulating function is required.

The Control of the Bile Flow. The bile is formed continuously by the liver-cells, but is passed into the intestine intermittently. It appears that almost any nervous, chemical, or vascular change in the splanchnic area may be attended by an outflow of bile. Thus the appearance of bile in the intestine does not necessarily coincide with active digestion, although as a matter of fact the conditions which lead to an abundant flow are more likely to be fulfilled then than at other times, since when no digestion is going on the alimentary tract tends to be quiescent. It has been supposed that the expulsion of bile is due, in part at least, to contractions of the muscular walls of the gall bladder, but just how important this action is cannot be said; in fact the function of the gall bladder is not at all clear; some animals (horses) have none, and persons suffer surgical removal of the organ with no serious ill-effects.

The Flow of Intestinal Juice is similar to that of gastric juice (see above) in being continuous, but greatly augmented during active digestion. The augmentation coincides with the beginning of active secretion of pancreatic juice, and is believed to be due to stimulation of the glands by the same hormone as evokes the flow of pancreatic juice, *i. e.*, secretin. The total secretion of intestinal juice is thought to amount to three liters (3 ½ qts.) or more each twenty-four hours; one function served by this copious flow is to restore to the lower part of the small intestine as much water as may be absorbed out of its upper portions in connection with absorption of food, thus keeping the intestinal contents as watery as proper function requires.

Digestive History of a Meal. We can summarize the whole process of digestion as well, perhaps, by following the course of an ordinary meal through the digestive tract as in any other way. We shall disregard the accessories, and consider only the nutrients proper, since, as we have seen, the digestive process concerns itself with these alone. The meal, then, is a mixture of carbohydrates, proteins, and fats.

In the mouth the food is reduced to a semiliquid, slightly alkaline mass, containing no large particles, by the combined action of chewing and mixing with the saliva. The salivary glands are reflexly excited to secrete their juice by the presence of the food in the mouth. The enzym of saliva, diastase, begins its digestive action on the starch, converting it to maltose. By the act of deglutition the food, when sufficiently mixed with saliva, is passed on to the stomach. If the chewing and swallowing of the food is attended with agreeable emotions, there is aroused a copious reflex secretion of gastric juice; the so-called "appetite" secretion.

The food *enters the stomach* in very much the same condition chemically as when taken into the mouth; a small amount of maltose added to it through the action of salivary diastase, and a correspondingly diminished amount of starch, being the only differences. That part of the food which is crowded down into the pyloric region begins at once to be churned by the peristaltic waves which sweep over that region; by the churning it is mixed with acid gastric juice. The food which remains in the fundic end of the stomach does not come into contact with acid; its reaction, therefore, continues alkaline, and the splitting of starch

by diastase goes on uninterruptedly. In the portion of food (chyme) which becomes impregnated with acid gastric juice the changes which the gastric enzyms, pepsin and rennin, are capable of producing take place. Rennin clots any milk that may be present; pepsin attacks proteins, converting them into proteoses and peptones. The gastric juice secreted under the stimulus of "appetite" is supplemented by an additional secretion, evoked chemically, either by a direct irritating effect of milk, meat juice, or digestion products of proteins, or by the action of a hormone which these call into being. Any fats present are liquefied, not by enzyms but by the stomach warmth. Finally as the hydrochloric acid of the gastric juice accumulates in excess the pyloric sphincter is stimulated to relax; the mass of chyme next to it is pushed through; and more material from the fundic end comes down to fill its place. Too much chyme is prevented from passing the sphincter at once by the powerful stimulus to contraction which is exerted on the sphincter by the acid chyme in contact with the upper intestine. The acid of this same chyme reacts with the prosecretin of the intestinal mucosa to form secretin, a hormone which is carried by the blood to the pancreas and excites it to activity.

The chyme which *enters the intestine* contains some, at least, of all the food stuffs originally making up the meal, and in addition maltose, proteose, and peptone. The strongly alkaline bile and pancreatic juice quickly neutralize its acid and the various enzyms of the intestinal tract act upon it. The diastase of the pancreatic juice converts to maltose all starch not affected by salivary diastase; the lipase of the same secretion splits the fats to fatty acid and glycerol; the trypsin of pancreatic juice, in co-operation with erepsin of the succus entericus reduces all proteins, including proteoses and peptones, to amino acids; the inverting enzyms, maltase, sucrase, and lactase, change all the double sugars, and therefore all the carbohydrates of the meal, to single sugars. The intestinal contents are churned and kept in onward progress by movements of segmentation and peristalsis performed by the muscular walls of the gut.

The Maintenance of Good Digestion. In the preceding paragraph the various activities essential to the proper performance of the digestive function have been outlined. If they are reviewed

carefully it will be seen that most of them, after the food reaches the stomach, are affected, directly or indirectly, by the conditions upon which depend the proper production of the appetite secretion of gastric juice. If, through anxiety or anger at mealtime, this secretion is inhibited, the whole sequence of the digestive process is upset. If the preliminary appetite secretion is inhibited little or no chemical secretion of gastric juice will appear; there is therefore not the necessary hydrochloric acid to stimulate the pyloric sphincter to relax, nor to react with prosecretin to form pancreatic secretin, should any food by any means get through into the intestine. Moreover, the same conditions which inhibit the appetite secretion inhibit also, as stated previously, the motions of the stomach and intestines. That indigestion usually follows the eating of meals under unfavorable emotional conditions is well known to all; the reason for it we have just seen.

The value of soups in aiding digestion is twofold. By exciting the appetite they help to arouse the appetite secretion; their content of meat juice is itself in some measure an excitant of the chemical gastric secretion, thus they are usually effective in starting the chain of events which make up the digestion of a meal. The practice of using them at the beginning rather than elsewhere in the meal, although long antedating our knowledge of their real value is thus seen to be physiologically sound.

CHAPTER XXX

THE ABSORPTION AND USE OF FOODS

General Statement. The digestive process, as we have considered it in preceding chapters, is purely one of preparation. Its completion finds the food still within the alimentary tract, but ready for the use of the Body. It is conveyed to the tissues, as we have seen (Chap. XVII), by the blood. The passage of digested food from the alimentary tract, through its walls, into the blood or lymph, is known as *absorption*. The use of the food by the tissues, since it involves chemical activities on the part of the tissues themselves, constitutes *metabolism*. The discussion of these two processes is the purpose of the present chapter.

Absorption from the Stomach. Although the food remains in the stomach for several hours after each meal, in fact is often not wholly discharged before the taking of another one, it appears that absorption from the stomach into the blood normally occurs to a very limited degree, if at all. This is one more instance of the way in which bodily functions are adjusted to work to the advantage of the organism. The fact that the digestive process is for no foods completed in the stomach affords sufficient reason why absorption should not take place there. We might suppose that the single great group of food stuffs not requiring digestion, the single sugars, could advantageously be absorbed from the stomach, but experiment shows that even they are absorbed very slightly unless in rather high concentration, 5 per cent, in which case the walls of the stomach do take them up rather rapidly; but at this concentration there is usually so much irritation as to cause vomiting, so that in practice no significant absorption is secured. The presence of alcohol in the stomach increases markedly its absorptive power, but this is at best a doubtful benefit, since the single sugars form ordinarily a minor part of the meal, and the other food stuffs are not ready for the use of the Body, and are wasted, therefore, if they are absorbed.

Absorption in the Small Intestine. The small intestine, being the chief and final digestive laboratory of the Body, is naturally

the place from which absorption most largely goes on. It is, in fact, specially adapted structurally, as is no other region of the alimentary tract, for the absorptive processes. The innumerable projecting villi, each containing a capillary network and a lymph-channel, afford a total absorbing surface many times greater than would the same area if lined with ordinary mucous membrane; they also, by projecting into the intestinal cavity, are brought more readily into intimate contact with the intestinal contents.

Nature of the Absorptive Process. Although the process of absorption, like that of gland secretion (p. 510) is presumably at bottom a physical one, involving filtration, osmosis, and dialysis, it cannot be accounted for to any considerable extent by simple application of those principles. Like gland secretion, absorption depends on metabolic activities of living cells, in this case the cells which form the innermost intestinal lining (columnar epithelium; Chap. XXVI). The difference between intestinal absorption and ordinary dialysis, for example, is illustrated by the fact that blood-serum placed in the intestine is absorbed completely through its walls into the blood so long as the mucous lining is alive and functioning, but fails to be absorbed if the cells are injured, as by sodium fluorid, or some similar poison. Since the blood-serum placed in the intestine has presumably precisely the same osmotic pressure and percentage composition as the animal's own it is difficult to see how purely physical factors could bring about the absorption.

Channels of Absorption. We noted above that each villus contains a capillary network and a lymph-channel. The absorbed food stuffs might pass, therefore, either to the blood-stream directly or by the lymph-channels be conveyed to the receptaculum chyli (p. 404), and thence by way of the thoracic duct enter the blood-stream at the great vein of the shoulder. The essential difference between these two pathways is that the intestinal blood-stream drains into the portal vein, and must pass, therefore, through the capillaries of the liver before reaching the general circulation, while the lymph-stream reaches the general circulation without first traversing the liver. The significance of these two pathways will appear presently.

The entire phenomenon of absorption from the small intestine

presents so many phases that it will be convenient to consider it in sections, one class of nutrients at a time.

The Absorption and Temporary Storage of Carbohydrates. Carbohydrate digestion reduces all foods of the class to single sugars. It is in this form, then, that they undergo absorption. However the process may be carried on it results in a flow of single sugars from the intestinal cavity into the blood-capillaries of the villi. These capillaries all drain, as previously stated (Chap. XIX), into the portal vein, which in turn passes to the liver and breaks up therein into the liver-capillaries (Chap. XXVI); so that all blood from the intestine, with whatever it may have taken up there, is forced to traverse the liver, and to come into intimate contact with the liver-cells, before it reaches any of the other living tissues of the Body.

The amount of sugar present in the blood of the portal vein is, of course, variable, there being a higher concentration at times when sugar is being actively absorbed from the intestine than at other times. Curiously, the blood flowing away from the liver, in the hepatic vein, is always found, normally, to contain a certain small percentage, about 0.10–0.12 per cent, of sugar, whether the sugar content of the portal vein is high or low.

It is evident that the liver must be able to store within itself the excess sugar that comes to it during active absorption from the intestine, and to give this out again between times. The sugar is retained in the liver, not as such, but in the form of glycogen or animal starch. The conversion of sugar into glycogen is a simple dehydration ($C_6H_{12}O_6 - H_2O = C_6H_{10}O_5$), and is easily performed by the liver-cells. An advantage of the change from sugar to starch seems to be to make the retention by the liver easier; sugar is too soluble to be held readily, whereas the liver can hold the glycogen without trouble. The liver is said to be able to hold 10 per cent of its weight of glycogen.

The use of the sugar is, as we have already seen, twofold, for fuel for the Body and as a source of lactic-acid precursor for the skeletal muscles. Oxidations are constantly going on in the living tissues, therefore there is a steady withdrawal of sugar from the blood, and the liver must be continually making good the depletion by reconverting some of its glycogen into sugar. That the sugar content of the blood is kept up at the expense of liver-glyco-

gen is proven by observations on fasting animals. A comparatively short period of starvation results in the disappearance of nearly all its glycogen from the liver. That in fact is the first fuel supply to be drawn upon in the absence of food.

The conversion of glycogen to sugar is performed by an enzym *glycogenase*, similar in action to salivary and pancreatic diastase, except that it carries the hydrolysis all the way to glucose, instead of halting at maltose.

Storage of Glycogen in the Muscles. These organs, as we learned when studying them (Chap. VII), perform their work through the oxidation of sugar, and since they are likely to be called upon for prolonged activity need to have immediately available a supply of their special fuel. Such a supply they have, in the form of glycogen, which makes up about 1 per cent of the weight of muscle tissue. This glycogen is, of course, derived from the sugar of the blood, so that the muscle-cells must have the same power that liver-cells have of changing sugar to glycogen and glycogen back to sugar.

The Relation of the Kidney to the Concentration of Sugar in the Blood. As we have seen, the sugar content of the blood remains practically constant all the time at a relatively low concentration, about 0.10–0.12 per cent. It is an interesting fact that the kidney, the great excretory organ of the Body, is so constructed that if for any reason the sugar content of the blood rises much above normal, to 0.17 per cent or more, the excess of sugar escapes from the blood through the kidney and appears in the urine. The kidney stands to the sugar of the blood in the relation of a spillway; it allows the concentration to rise just so high, but no higher. This property of the kidney makes such a storage mechanism for sugar as we have described virtually necessary to the Body, since without it the tissues could not be provided with fuel at once continuously and economically.

The Assimilation Limit. Alimentary Glycosuria. The ability of the liver to convert into glycogen the sugar delivered to it by the portal vein is not without limit. If the absorption from the intestine is so rapid as to raise the sugar content of the portal blood to an abnormally high point, the conversion of sugar to glycogen fails to keep pace and the excess escapes in to the hepatic vein and so into the general circulation. Should this excess be

sufficient to raise the sugar percentage of the blood above 0.17 per cent there is excretion of sugar from the kidney, a condition known as *glycosuria.* It is found that the rate of absorption of sugar depends chiefly on how much of it is present at one time in absorbable form in the intestine. Thus if large amounts of single sugar are eaten the essential condition for excessive absorption is likely to be fulfilled. Honey, a sweet containing considerable single sugar, is thus apt to cause glycosuria if too freely eaten. The greatest amount that can be eaten without causing glycosuria marks the *assimilation limit.* The other carbohydrates, since they require digestion before they are absorbed, are less apt to give rise to too rapid absorption. It is found, however, that there is a great difference in the amounts that can be taken without exceeding the assimilation limit. The inversion of milk-sugar gives rise to a special single sugar, *galactose,* which is not converted into glycogen, but circulates in the blood until used. The assimilation limit for milk-sugar is correspondingly low. Starch is digested so slowly that the assimilation limit for it is quite difficult to exceed. Glycosuria resulting, not from disease, but merely from overconsumption of carbohydrates, is called *alimentary glycosuria.*

Other Types of Glycosuria. An analysis of the carbohydrate-storage mechanism just described reveals three points where an upset of the normal sequence might give rise to glycosuria; and three corresponding varieties are known. The three conditions which may cause glycosuria are: (1) A disturbance of the mechanism which controls the rate of conversion of liver-glycogen into sugar, so that more is poured into the blood than the tissues have occasion to use; (2) a diminution in the consumption of sugar by the tissues, so that more accumulates than the liver can store; (3) an alteration of the kidney such that it excretes all the sugar that comes to it, and thus drains sugar from the blood continuously. Much insight into the working of the carbohydrate-storing mechanism, as well as the use of carbohydrates by the Body, has been gained by study of these three forms of glycosuria.

Glycosuria from Disturbance of the Liver Function. Emotional Glycosuria. It has been shown that injury to a definite point in the medulla leads to an increased conversion of glycogen to glucose by the liver; the process is spoken of as "mobilization of sugar." Since this sugar is poured out into the blood in excess of

the requirements of the tissues glycosuria results. The connection between the "glycosuria center" in the medulla and the liver-cells is by way of the thoracico-lumbar autonomic system; the nerve path is in the splanchnic nerves; hence after these nerves are cut irritation of the "glycosuria center" no longer causes sugar to be mobilized.

In this nervous control of the output of sugar by the liver we perceive a mechanism for adjusting the delivery of fuel to the tissues to correspond with their requirements; increased activity of the tissues involves increased consumption of sugar, with a greater call upon the liver for supplies, and, as we know, the tissues most involved, the muscles, send into the medulla streams of afferent impulses whenever thay are active, which would serve to excite the center. In corroboration of this idea it may be stated that certain diseases of the central nervous system in man result in an upset of the liver function of precisely this sort.

Recent observations have brought out the interesting fact that this "nervous control" of the conversion of glycogen to sugar by the liver, although in large part direct, may operate in part through the intervention of the hormone adrenin. Some time ago the discovery was made that during great emotional excitement sugar is apt to appear in the urine. A test was made on the members of the football squad of a great university immediately following the crucial game of the year. Of the men examined, players and substitutes, many showed pronounced glycosuria. This fact, in conjunction with the known outpouring of adrenin in times of stress, suggested a definite relationship, and the demonstration was shortly afforded that increased production of sugar from liver glycogen may be brought about in experimental animals as the result of stimulation by the hormone. The process as a whole we recognize as a part, and an important part, of the general emergency reaction of the Body. At a time when the utmost muscular exertion is likely to be demanded it is imperative that there be no failure from a shortage of fuel. The flooding of the blood with sugar as the result of the direct nervous stimulation from the "glycosuria center," supplemented by the stimulus from the outpouring of adrenin, assures that the fuel supply for the laboring muscles shall be ample. That there is an *overproduction*, so that much passes out by the kidneys and is wasted, merely

emphasizes the general principle that in time of emergency economy is sacrificed, the resources of the Body being expended lavishly toward successful meeting of the immediate situation.

Glycosuria from Inability of the Tissues to Use Sugar. Diabetes Mellitus. This condition, the usual pathological cause of glycosuria, and unfortunately not of rare occurrence, has been much studied, chiefly because it involves the relation of the tissues to their chief fuel supply, sugar, and a complete understanding of the disease should throw much light on the mechanism of the consumption of fuel by them. The presence of sugar in the urine is only one of the symptoms of diabetes mellitus. A symptom of equal importance is the muscular weakness, and particularly the lack of endurance, which results from the failure of the tissues to make use of their fuel supply to advantage.

A very interesting feature of this condition is that it can be induced experimentally in a quite unexpected way, namely, by injuring or removing the pancreas. Complete destruction of this organ is followed by an apparent total loss of the power of the tissues to use sugar; there is excessive muscular weakness, and death occurs in a few days after the operation. The effects of partial destruction are less severe; in fact no symptoms appear unless fully three-fourths of the gland are destroyed. The function of the gland in connection with the prevention of diabetes is wholly independent of its function as a digestive gland. The duct of the pancreas may be tied without the production of diabetes, or the gland may be transplanted from its usual location to some other, quite abnormal one, where, if it lives and establishes connections with the circulation, it suffices to prevent diabetes perfectly.

Insulin. This function of the pancreas has lately been shown definitely to be a hormone action. The hormone is not produced by the same cells of the gland as form digestive enzyms, but by certain peculiar groups of cells imbedded in the gland, known as the *Islands of Langerhans*. The anatomical juxtaposition of "Island" tissue with the pancreas as a whole has no significance, so far as can be told, since in fishes the Islands are separate organs.

Although it has been virtually certain for a good many years that the Islands of Langerhans produce a hormone efficient in preventing diabetes mellitus, the actual proof has been obtained

only within the last half decade. The difficulty was that when ordinary water-extracts of pancreas were made the proteolytic enzym also present in the extracts destroyed the hormone. The blood supply to the pancreas happens to be so distributed that the enzym-secreting tissues can be deprived of blood by tying off certain vessels, in experimental animals, without interfering with the nourishment of the Island tissues. After this is done the enzym-forming tissues degenerate, leaving the Island tissues as the only ones functioning. When an animal that has been prepared thus is killed and an extract of its surviving Island tissue made, the extract is found to contain the hormone in abundance. The name *insulin* has been assigned to the hormone, to indicate its origin from Island tissue. Immediately upon the first testing of an extract prepared as above it was clear that the long-sought hormone had been found. The event was of great importance, for pancreatic diabetes has claimed many victims, and caused much suffering, hence the discovery of the hormone effective in preventing it forecasted great benefit to mankind. To make the discovery of practical value it was necessary to find a method of extraction applicable on a large scale; in effect one that would enable pancreas tissues from packing-house animals to be used as the source of supply. The method that gave the desired result was to treat fresh pancreatic tissue with alcohol, which renders the enzyms inactive without affecting the hormone. As a matter of fact the discovery of this differential action of alcohol ranks in practical importance with the original discovery of insulin, since it has made the hormone available on a large scale so that the majority of diabetics may receive treatment. The alcohol extracts, prepared as indicated above, are purified and standardized, ready for use. Insulin cannot be administered by mouth, since the digestive enzyms destroy it. Subcutaneous injection has to be used.

Action of Insulin. When there is insulin in the blood the tissues take up sugar actively, and more actively the higher the concentration of the hormone. Why this is so is at present unknown. The effect is that when there is no insulin present no sugar is taken up, and if insulin is deficient less sugar is taken up than the tissues would normally utilize in their metabolism. Furthermore, if more insulin is introduced into the blood than is

present normally the tissues take up sugar to excess, reducing the concentration in the blood from the usual minimum of about 0.10 per cent, to as low as 0.045 per cent. Striking symptoms develop in man as the concentration of blood-sugar falls; they proceed from extreme hunger through feelings of weariness and muscular tremor to convulsions, which would terminate fatally if allowed to continue. The symptoms can be relieved very promptly at any stage by simple administration of glucose, to bring up the concentration of the same in the blood to a safe level. The actual tissues to suffer when the concentration of blood-sugar falls are those of the central nervous system. The cause of the fall in blood-sugar is that some of the tissues take it up too actively, but we do not know whether the symptoms are due to the fact that the nervous tissues have become overcharged with sugar or to a sudden and severe lack of the fuel on their part due to the depletion of the blood by other tissues.

All that insulin does, so far as we know, is to enable the tissues to take up sugar as indicated above. There are two dispositions that the tissues may make of what they take up; they may oxidize it, either in basic or functional metabolism (the amount used in basic metabolism depends on the quantity of available hydrogen transporters (in effect thyroxin; pp. 26, 216), since the vigor of basic metabolism is determined, not by the quantity of fuel available, but by the concentration of hydrogen transporters; the amount used in functional metabolism depends on the stimulation to which the tissues are subjected, and again not on the quantity of fuel provided); or they may store it as glycogen or fat (see below). Lack of insulin obviously interferes with ability to store sugar as much as with the ability to oxidize it, hence we find that in diabetics the liver and muscles are poor in glycogen.

Relation of Insulin Deficiency to Glycosuria. Since the tissues of a person deficient in insulin cannot take up sugar in normal amounts, either for utilization or storage, if carbohydrates are taken in the food sugar is bound to accumulate in the blood up to the point at which the kidneys no longer retain it, and beyond that point to escape in the urine. Thus glycosuria is inevitable if carbohydrates continue to be eaten. The obvious way to obtain relief is to cut down the intake of these nutrients. Within limits to be considered later this is feasible, and generally done in cases

of diabetes, but when the insulin deficiency is severe it is often impossible to avoid glycosuria, even though no carbohydrates are eaten. The reason is that many of the amino acids yield glucose when they decompose in the Body (see p. 536), and when the diet is made carbohydrate-free either proteins are eaten in such quantity that their glucose residues cause glycosuria, or the patient is starved to the point where his own body-proteins break down into amino acids, some of which, in turn, yield glucose.

Glycosuria of Kidney Origin. The injection of a certain drug, *phlorhizin*, into the circulation is followed by a glycosuria which is due chiefly, although perhaps not wholly, to alterations in the kidney. These are of such a sort that the kidney-cells, instead of permitting only sugar in excess of 0.17 per cent to escape, pass all that comes to them. The result, of course, is a great waste of this valuable fuel, requiring greatly increased consumption of carbohydrates to make it good. This form of glycosuria has been produced experimentally in animals, for purposes of study, but occurs rarely, if at all, as a disease of man.

The Absorption of Proteins. We have learned that the digestive process splits proteins into their constituent amino acids (p. 493). The advantage of this is obvious, when we recall the fact that an important function of proteins is to repair tissue waste, and the further fact that to do this the food protein must be converted into the characteristic tissue protein of which it becomes a part. We saw in Chap. I (p. 20), that the difference between one protein and another is in the number, proportions, or arrangement of the amino acids which make up their molecules. While the food proteins, as such, would not serve for tissue repair, the amino acids of which they are composed are precisely what the Body needs for rebuilding its own substance. Furthermore, the different tissues must differ somewhat in the constitution of their characteristic proteins, and for the repair of all the different tissues a mixture of amino acids is evidently much more useful than a small number of undigested food proteins could possibly be.

There is abundant evidence that the digested amino acids are absorbed directly into the blood-stream, and not into the lacteals. This has been proven by inserting a tube into the thoracic duct of an animal and draining off all the lymph produced during the absorption of a protein-rich meal. No increase in the percentage

of nitrogen (the characteristic element of proteins) could be detected in the lymph; conclusive proof that the amino acids do not follow that pathway. Moreover, chemical methods recently devised have shown the presence of amino acids in the blood-stream, and that during the absorption of a meal of meat they are increased in amount. The use the Body makes of these amino acids will be considered in detail in a later paragraph, as will also the relation of the liver to them.

The Absorption of Fats. The result of fat digestion is to split the fats to fatty acid and glycerol. The glycerol is soluble in water, and is therefore taken up directly by the cells of the intestinal lining. Fatty acids are not soluble in water, but they react with the alkali furnished by the pancreatic juice and bile to form water-soluble soaps. These latter are then absorbed into the lining cells of the intestine. For a long time it was thought that with the aid of bile fatty acids might be absorbed without being first changed into soap, but the discovery that mineral oils, which are not saponified in the intestine, are not absorbed, seems to prove that saponification is necessary before absorption can occur.

If the flow of bile is cut off (a condition known as obstructive jaundice, often due to inflammation of the bile duct) fats are neither digested nor absorbed, but remain in the intestinal tract. The result is interference to some extent with the digestion and absorption of other nutrients, since the unabsorbed fats tend to smear themselves over the other constituents of the chyme in the intestine. The stools take on a peculiar "clay-color" indicative of failure of fat absorption. It is probable that this phenomenon is due largely to the relative inactivity of pancreatic lipase in the absence of bile, although it may be that the absorption of soaps is dependent to some extent also on the presence of this substance in the alimentary tract.

After the absorbing cells of the intestinal wall have taken up the fatty acid and glycerol these are recombined within the cells into fat. The presence of fat droplets in the absorbing cells can be demonstrated microscopically. We know that the fat droplets are not absorbed as such, but are formed after their constituents have been separately taken up, because these fat droplets are always observed in the part of the cells away from the intestinal cavity, and never in the part next to it; also because we know that

the digestive splitting to acid and glycerol takes place, a meaningless process if not necessary to absorption.

The greater part of the fat finds its way into the circulation by way of the lymph-channels of the villi, the lacteals, and the thoracic duct, entering the blood-stream at the point of emptying of the thoracic duct in the large vein of the shoulder. Fats alone, of all the food stuffs, take this course, and we may suppose the difference to mean that the liver has no special function to carry out in connection with the fats as it has for carbohydrates and proteins. Therefore the fats are shunted into another course which carries most of them into the blood-stream without having first to traverse the liver.

Absorption from the Large Intestine. The mass that passes through the ileocolic valve into the large intestine contains comparatively little absorbable food material. The carbohydrates and fats are very completely removed during the passage of the small intestine, and fully ninety per cent of the proteins as well. There remains for the large intestine, then, only the absorption of the protein residue and the absorption of water. It is probable that this latter function, that of absorbing water, is in reality the chief one possessed by the large intestine. There is considerable absorption of water in the upper portion of the small intestine but this is made good by secretion of intestinal juice into the lower segments (p. 517), hence the intestinal contents pass the ileocolic valve as liquid as when leaving the stomach. This maintenance of a liquid consistency is, of course, essential to the absorptive processes, and it is only after all absorbable food has been removed that the water, which is also needed by the Body, is taken up.

The Food Requirement of the Body. If we know how much energy the Body liberates in a day, and how much tissue breakdown it suffers, we ought to be able to estimate how much energy-yielding food, and how much tissue-repair food is required daily; assuming, of course, that we know the amount of energy yielded by definite weights of food stuffs. By the use of devices called *calorimeters* the total energy liberation of the Body per day has been determined under various conditions, and the energy content of the various foods has also been found. We learned in a previous chapter (p. 434) that a unit of heat energy commonly used in physiology is the *Calorie;* the amount of heat required to raise

1,000 grams of water through 1° centigrade. In terms of this unit the energy output of man in 24 hours averages from about 2,400 Calories for men of sedentary occupation to 5,000 Calories for those doing heavy manual labor. The energy yield of the various foods is as follows:

Carbohydrates	4.1 C. per gram.
Proteins	4.1 C. " "
Fats	9.3 C. " "

It is therefore a matter of simple calculation to determine how much of any one food stuff is needed to supply the required energy, or to arrange suitable mixtures of the three. By reference to the table of food compositions (Chap. XXV), the amounts of actual food materials needed can be found.

The Protein Requirement of the Body. Before proceeding with a further discussion of the energy relationships of the Body it will be well to consider the tissue-maintenance requirement, which as we have seen, is wholly a protein need. In order to analyze this requirement intelligently we need to know, first of all, what use the Body makes of protein, and second, how much is required. We have already seen that protein can be oxidized in the Body with the liberation of energy, and constitutes, therefore, a good fuel. In this respect, however, it is in no degree superior to the other nutrients, fats and carbohydrates. Our special interest in it is for the function which it alone can exercise, that of making good tissue wear and tear.

Since protein is the only food stuff that contains nitrogen we can tell how much of it is used up in the Body by measuring the amount of nitrogen eliminated (p. 108). All except a very small portion (roughly 2 per cent) is discharged in the urine. Chemical tests of the urine will furnish us, then, with the data we seek. Evidently if a man abstains wholly from food for a while all the nitrogen in his urine must come from tissue breakdown. We have a means, thus, of finding out how rapidly this breakdown occurs. A moment's thought will show us, however, that the tissue breakdown in complete starvation is not necessarily the same as in ordinary life. When no food is eaten the *energy requirements* of the Body must be met at the expense of its own tissues; particularly in prolonged starvation, when the stored fuels, fat and glycogen

have been used up; so that in addition to the usual loss of substance by wear and tear there is a further consumption of material as fuel. To get at the amount of tissue breakdown under ordinary conditions by this method the starvation must not be complete. The subject must be given abundant supplies of fat, carbohydrates, and essential accessories, but no proteins. When this is done the nitrogen eliminated from the Body can be assumed to represent the normal tissue breakdown. Experiments conducted along this line have shown that in an adult man of ordinary size (70 kilos, 154 lbs.) the protein lost from the Body daily by tissue wear and tear amounts to about 20–25 grams ($\frac{2}{3}$–$\frac{5}{6}$ oz.). Theoretically it should be possible to sustain life indefinitely on a diet containing this amount of protein, provided adequate fats and carbohydrates for the fuel requirements of the Body are also furnished. This theoretical minimum of protein does not agree at all well with the amounts of protein actually consumed. In fact dietary studies show that most people take four to five times this amount. The great discrepancy between the amount of protein theoretically required and that actually ingested has occasioned a great deal of discussion among dietitians as to whether the human race is habitually consuming proteins to excess. Since proteins are expensive food stuffs the question is one of great economic importance.

Numerous experiments have been performed to see what is the effect of cutting the protein intake approximately to the theoretical minimum. In all the early experiments along this line when the protein content of the diet was reduced to about 35–40 grams daily, a figure well above the theoretical minimum, the tissue wear and tear was no longer made good completely. This was evidenced by the daily elimination from the Body of more nitrogen than was taken in. The only possible source of the excess was from breakdown of the Body's own tissues. There was also a steady loss of body weight. When an explanation of this was sought it was found that the chief difficulty lay in the manner of administering the protein. This substance when taken with the diet in the usual rather large amounts functions in part to replace worn-out tissues and in part, as we have seen, as fuel for supplying energy, the latter use being made of all surplus after the tissue repair has been provided for. The wear and tear of

tissues goes on throughout the twenty-four hours of the day. The ordinary method of taking the protein, on the other hand, is in three meals during the daytime portion of the day. When the consumption is cut down to a low level evidently if there is any use of protein as fuel a shortage for tissue repair is likely to occur. When the protein is ingested in connection with the usual meals there is absorbed into the Body after each an amount which is in excess of the immediate needs for tissue repair, and accordingly some is used as fuel. The result is that before the time for the next meal arrives all the absorbed protein is used up and there is none to carry on the work of tissue repair. To avoid this the experiment was tried of dividing the protein into six equal parts and administering one part every four hours. When this was done, so that there was a practically continuous though small absorption of protein into the Body, it was found possible to make good completely the tissue breakdown with an amount of protein very little in excess of the theoretical requirement.

The Replacement Value of Different Proteins. Obviously to make good the wear and tear of the tissues with the least possible amount, the proteins ingested must correspond as closely as possible in composition with those of the Body itself. We have already noted (p. 529) that the difference between different proteins are in the number or relative amounts of amino acids present. These differences are in some cases very pronounced. In general meat proteins resemble those of man more closely than do proteins of vegetable origin. Any protein that contains only a small proportion of some amino acid present in human protein in large proportion must evidently be fed in sufficient amount to satisfy the requirement for that particular amino acid. The other constituents, meanwhile, are in excess and afford a surplus to be used as fuel. It appears that the Body possesses a limited ability to convert some kinds of amino acids into others, but this is applicable to so few of the many which make up the protein molecule as to have little practical bearing.

Maintenance Proteins and Growth Proteins. Evidently, from what has been said above, any protein that is completely lacking in some essential amino acid or acids cannot serve to replace worn-out tissues. Such a protein is ordinary table gelatin. This is a protein derived from bone and connective tissue (p. 57). It is

deficient in three of the amino acids which are essential to living protein (tryptophan, tyrosin, and cystein). No matter how much gelatin may be included in the diet, if there is not provided also some protein which contains these essential acids wasting of the tissues will occur.

Related to this fact is the even more remarkable discovery that there are certain proteins which are fully adequate for the maintenance of the Body, but will not suffice for the formation of new tissues. Young animals fed upon diets whose protein components are of this character will maintain a constant weight, but will not grow. A good example of such a protein is *gliadin*, one of the proteins of wheat. This protein lacks the amino acid, *lysin*. The conclusion drawn from this observation is that the lysin which is one of the constituents of living protein is not involved in the processes of tissue breakdown. After the tissue is once formed, therefore, it does not require continual supplies of this substance. No new tissue can be made, however, unless lysin is provided. A curious incidental discovery in connection with the experiments by which this was established was that the rats which were used as subjects could be maintained in health with the weight and bodily dimensions of young animals for months after they would have become full-grown on an ordinary diet. If then they were changed from maintenance proteins to proteins that were adequate for growth they promptly began growing and presently attained full size. The significance of this is that the ability to grow is not restricted to the early periods of life and does not come to an end with the attainment of a certain age.

Fuel Protein. We have learned that proteins are absorbed from the digestive tract into the blood as amino acids. Of these a portion are destined to provide for tissue repair and growth. The excess is used as fuel. The nitrogenous portion is virtually devoid of value as a source of energy. To fit the remainder to serve as fuel the nitrogen-containing radicals are dissociated from the molecules, leaving non-nitrogenous residues of high energy value. This process of setting aside the nitrogenous radicals is known as *deamination*. It is carried on by the tissues generally, and occurs wherever they or any one of them are in receipt of amino acids in excess of the amounts needed to make good protein losses. The further history of the nitrogen-containing radicals will be

considered in a later chapter (p. 549). The non-nitrogen residues join themselves with the other energy-yielding food stuffs and will be discussed together with them

Should the Diet Include Much or Little Protein? We have seen that it is possible to maintain the tissues adequately upon a diet containing only a fraction of the amount of protein ordinarily taken. Are we to conclude from this that the human race eats too much protein? To this question no final answer can be given at present. Eminent dietitians have argued on both sides of it. One consideration that has been suggested as probably significant is that the low protein diet, although adequate for immediate maintenance, does not afford the Body sufficient reserve vitality to place it in the best situation for resisting infections or other debilitating influences. Emphasis has also been placed on the fact that the poorer inhabitants of Bengal, who live of necessity on a low-protein diet, are deficient both in strength and endurance. Conservative students of the subject are inclined to the opinion that our present dietary habits, based as they are upon centuries of experience, are probably in the long run better suited to our needs than radically altered dietaries, which may be theoretically sound, but lack the confirmation of long experience.

The allowance of protein in standard diets varies from 80–90 grams daily, which is the average amount consumed by American College students, to the 115–120 grams considered by some European dietitians suitable for the European laborer. In contrast with these figures are the allowance of 40–60 grams proposed by the advocates of a low-protein diet. While we may properly adopt a conservative attitude with reference to the low-protein controversy, we are not thereby justified in going to the opposite extreme. Excessive consumption of meat, particularly by people who lead sedentary lives, undoubtedly is attended by various evils, although most of these are referable to other causes than overconsumption of proteins.

The Liberation of Energy in the Body. We have seen that all the energy liberated by the Body can be expressed in terms of heat-units, but it is not to be concluded, therefore, that heat energy is the only form manifested by the Body. As a matter of fact the Body undoubtedly converts the potential energy of the food into at least three forms of kinetic energy; *chemical,*

the carrying on of the digestive and other chemical processes of the Body; *mechanical*, the working of the skeletal muscles, as well as of the heart, the muscles of respiration, and the muscles of the viscera; and *thermal*, the direct production of heat by oxidation processes. This latter form of energy, although far exceeding in amount both the others together, may be looked upon as in large degree a by-product of the mechanical work of the Body, and arising through the inefficiency of the Body machinery. We know that most of the heat of the Body is produced in the muscles, and that though these are producing some heat even when at rest, they produce enormously more when they are active. A characteristic of all machines is that they work more or less wastefully; not all the energy imparted to them appears again as useful work; the part that is lost, moreover, appears always as heat. In the Body there is this same inability to convert food energy into mechanical energy without there being at the same time a large heat production.

Studies of the metabolism of the Body must necessarily take into account these two main forms in which the energy of the food is manifested. For physical reasons which need not be considered here all muscular and chemical activities occurring wholly within the Body manifest themselves ultimately to the exterior in the form of heat. The total energy turnover of the Body can be determined, therefore, if the external mechanical work and the entire heat output can be measured. Theoretically these should exactly balance the energy content of the ingested food. Metabolism studies are devoted in part to demonstrating that this balance actually exists, and in part to determinations of the individual factors concerned.

Basal Metabolism. A necessary starting point for any study of energy manifestation in the Body is the determination of the amount liberated when the Body is as *inactive* as possible. The metabolism which gives rise to this energy represents that which is essential to the life processes. It is known as the *basal or resting metabolism*. It includes the sum total of the basic metabolism proper (p. 24) plus a certain functional metabolism essential to life (contractions of the heart muscle and the muscles of breathing, movements of the alimentary tract, and the like). Its energy all appears in the form of heat. As measured in an adult man of

average size, who eats nothing during the day of observation, it amounts to about 1,700 Calories (p. 434). The necessary activities of eating and digesting enough food to maintain the Body involve an expenditure of about 10 per cent additional energy, bringing the total practical basal metabolism up to about 1,870 Calories per day. Any energy liberation in excess of this amount must represent either actual muscular work or the by-product of heat which always attends it on account of the inefficiency of the muscles.

We shall see in the chapter on Heat Regulation (Chap. XXXII) that the Body makes very good use of this by-product of heat in keeping itself at a proper temperature the year round, and so the extra amounts of food we have to eat on account of the inefficiency of our bodily machines are not wholly wasted after all.

The Metabolism of Muscular Work. The total energy turnover per day of any individual is made up, as we have just seen, of his basal metabolism, together with the metabolism of his active muscles. The first factor is usually nearly constant for any given individual; the second is extremely variable. Some average figures may, however, be presented. If we reckon the muscular efficiency at 20 per cent, every Calorie of energy manifested in the form of muscular work means a consumption of 5 Calories altogether, and a liberation of 4 Calories as the by-product of heat. A man who leads a decidedly sedentary life, making no more movements than necessary, is calculated to do an amount of work in a day equivalent to about 40 Calories (120,000 foot-pounds). This work consists in large part of the labor involved in the maintenance of the sitting and standing positions. The performance of 40 Calories of muscular work requires, on account of the bodily inefficiency, previously noted, an energy liberation of 200 Calories. This, added to the practical basal metabolism of about 1,900 Calories, brings the total to 2,100 Calories. When allowance is made for a moderate amount of exercise; no more than must be taken if good health is to be maintained; the daily metabolism amounts to 2,500 Calories. This figure is believed to represent the average for adults of all classes other than manual laborers. An interesting fact is that calculations of the average daily metabolism per individual of the inhabitants of cities, based on estimates of the amounts of food brought in each day to the

markets, indicate this same figure, 2,500 Calories, as the average metabolism for the city dweller. The energy liberation of the manual laborer varies greatly, of course, with the nature of the toil. The range is usually set at 3,500 to 5,000 Calories per day. The latter figure probably represents a high limit which is rarely exceeded by any worker day after day for long periods, although trained men may show a much greater metabolism for a day or two. For brief spurts the figures may go much higher. The astonishing figure of 30 Calories per minute has been reported as attained by trained athletes (oarsmen) in a short race (6–8 minutes).

The Relative Food Values of Proteins, Carbohydrates and Fats. Disregarding the use of protein as a tissue-repairer, and considering all three varieties of food simply as furnishers of energy, we may inquire whether any one of them is superior to the others, or whether any particular proportion of the three food stuffs is specially desirable. From the purely mechanical standpoint there is evidently no choice among them; the Body requires 2,500 or more Calories of energy each day; each food stuff yields definite amounts of energy; therefore all we have to do to supply the Body's requirement is to eat enough grams of one or the other food stuff, or of a mixture of them. The answer to the question goes back, then, to other considerations than that of the energy content of the foods. The first of these is the matter of relative digestibility and absorbability; it is of little avail to eat a food if it fails to be properly digested and absorbed. Experiments have shown that carbohydrates, exclusive, of course, of cellulose, are the most completely absorbed of all foods, 97 per cent of the amount eaten finding its way into the Body; fats come next in order, 94.4 per cent being absorbed; proteins are taken up least completely of all, the Body getting only 92.6 per cent of the protein eaten. There are also differences of digestibility and absorbability of different foods within the same class, the protein of lean meat, for example, being more readily digested and absorbed than that of beans and peas. Cheese, which contains the highest per cent of protein of any common food, has a reputation, perhaps undeserved, for indigestibility. Graham bread is, by many, supposed to be more nutritious than white. It is true that graham flour contains a higher percentage of protein than does white flour, but the extra protein of the graham flour is in the bran, whence the human

digestive process fails to extract it; so as a matter of fact white bread yields more actual nourishment to the Body than does graham. The special importance of graham flour or of whole wheat is in the roughage and possible vitamins it contains. Some fats are much more digestible than others; olive oil and pork fat, for example, are more completely utilized by the Body than is mutton fat. Fat of any sort, taken in the meal with other foods, seems for some reason to delay the whole digestive process, and the delay is greater the more fat is present. For this reason it is desirable to limit somewhat the amount of fat used.

Another question which may affect the choice of foods is the degree to which they tax the excretory organs of the Body. We have seen that fuel proteins yield a nitrogenous residue which must be got rid of by the excretory organs. There seems to be a rather general belief that this task constitutes a somewhat serious strain upon these organs, and if it does tend to throw upon them excessive labor it is clear that the consumption of proteins ought on this account to be kept as low as possible. The idea that the excretory organs are endangered by ordinary amounts of protein in the diet is not sustained by any very convincing evidence. In fact there is at least one race of men, the Eskimos, in which huge consumption of flesh proteins is the rule and in which no tendency to gout and the other diseases ordinarily attributed to overuse of meat is discoverable.

In the matter of cost, which must also be taken into consideration, carbohydrates have a marked advantage over the other food stuffs. For example, bread, which is chiefly carbohydrate, yields, dollar for dollar, about ten times as many Calories as lean beef, a protein. The cheapest proteins are the vegetable ones; a given weight of protein costing about five times as much when bought as beef as when purchased in the form of beans.

Still another factor to be taken into account is the appetizing quality of the different foods. The frequent dependence of the whole digestive process upon a proper initial appetite secretion of gastric juice emphasizes the importance of the use of appetizing foods. Boiled meat contains as much nourishment as the same weight of roasted meat, but the former is less desirable as a food because the process of boiling extracts from it the substances which impart to meat its flavor. Eggs are exceedingly nutritious, but to

some people they are practically valueless as food, because they inspire aversion rather than appetite.

Analyses of large numbers of dietaries have brought out the interesting fact that Americans select, on the average, a diet in which the nutrients are distributed so that about 12–14 per cent of the total energy is taken in the form of proteins, 27–32 per cent in the form of fats, and the remainder in the form of carbohydrates. Recurring to the data on energy-values of the different nutrients on p. 532, and adopting for the purposes of the illustration a total metabolism of 2,500 Calories, this is found to imply a protein consumption of 73–85 grams, a fat consumption of the same range of weights, *i. e.*, 73–85 grams, and a carbohydrate consumption of 330–370 grams. A convenient round number to remember is that 200–210 grams of actual nutritive material are consumed for each 1,000 Calories of energy liberated in metabolism (assuming the average distribution of nutrients). Allowing for the high percentage of water in most food stuffs this is about equivalent to a pound of mixed food as eaten at the table. One can thus determine his metabolism roughly by weighing his food and allowing 1,000 Calories to the pound.

The Specific Dynamic Action of the Nutrients. A fact of metabolism that has attracted a good deal of attention is that during the period of active absorption of any nutrient the resting metabolism is greater than at other times of equal bodily activity, and even greater than can be accounted for by making suitable allowance for possible energy requirements of the absorptive processes. This is known as the "specific dynamic action" of the nutrients. It appears that a special stimulus of some kind is afforded by the entry of nutrients into the Body in relatively large amounts. The effect is most marked in proteins; in fact only with these does it have much practical significance. The metabolism is so augmented, and the consequent heat-production so increased, by abundant eating of proteins, as to amount to an important factor in keeping the Body warm in winter (p. 578). Furthermore, under the stimulus of active protein absorption the Body may be caused to metabolize stored fats, thus reducing body-weight. This feature accounts for the use of high-protein in "anti-obesity" diets.

The Nutritive Value of Gelatin. This protein, as stated above (p. 534), lacks some of the essential constituents of cell proteins,

and cannot, therefore, serve as a tissue-restorer. We can imagine, however, that it ought to satisfy the Body's demand for protein fuel, and so be substituted for the major part of the protein of the diet. Various attempts have been made to substitute gelatin for proteins in this way, and it seems to be highly efficacious in satisfying the Body's protein-fuel demand. But curiously gelatin can be used thus for only a few meals; presently there is a revolt of the appetite against it and no more can be eaten. Experiments have shown that dogs will starve rather than take continuously a diet whose chief constituent is gelatin.

The Special Metabolism of Fats. Fats are very useful fuel foods. Their energy content is twice that of the other nutrients. As we saw in an early chapter (p. 118) they can serve as sources of muscular energy. At that place the statement was made that certain evidence exists, unfavorable to the idea that they are converted into sugar before being utilized. This evidence is of a technical chemical nature; the important feature of it for our present purpose is that it includes the finding that in the process of decomposition of the fat molecules, preparatory to their oxidation, one molecule of a simple organic acid (aceto-acetic acid) is formed for each molecule of complex fatty acid oxidized. In case sugar (or sodium lactate, p. 117) is being oxidized at the same time, in the proportion of as much as one molecule of sugar to each one of fatty acid (on an ordinary diet the proportion is about ten times this), the aceto-acetic acid is also burned, and used by the Body as a source of energy; should the tissues be unable to burn sugar to the above extent, either because they cannot take it up (diabetes) or because none is available (prolonged starvation) the aceto-acetic acid remains unutilized, and becomes in effect a metabolic waste-product. A portion of it is converted into *acetone*, which is exhaled in the respired air, giving a characteristic "diabetic" odor to the breath; another portion is likely to be changed into highly poisonous β hydroxybutyric acid; when this latter change occurs in considerable degree a comatose state (diabetic coma) supervenes, frequently terminating in death. It is this ever-present danger that makes the nourishment of diabetics difficult, since they cannot utilize carbohydrates, nor proteins, which are in effect mostly carbohydrates after deamination (p. 536), and use fats only with the above described hazard con-

stantly impending. It is clear that the discovery of insulin, and of a means for producing it on a large scale, has solved a problem that appeared almost insoluble prior to the discovery.

Principles of Dietetics. From the various considerations presented above we may summarize the general rule that the choice of food should be such as to yield sufficient protein for the Body's protein requirement, without containing an amount so excessive as to throw an undue burden on the excretory organs (in practice about 70–100 grams); that the amount of fat should be such as to provide about 30 per cent, more or less, of the total energy consumption; and that enough carbohydrate should be added to bring the sum total up to the Body's energy requirement; finally, that the most appetizing foods obtainable within a reasonable limit of cost should be selected. Fortunately for the well-being of the race, mankind has always selected just such a diet under no other guidance than his appetite and his means, and these, to a healthy person, make trustworthy guides, so long as they are accompanied by temperance as a third.

The importance of *dietetics* as a science is chiefly in connection with the feeding of the sick, or providing for the maintenance of large numbers of individuals, as in armies or public institutions, where a slight error in selecting food, in greater amounts, or at greater cost than needed, amounts in the aggregate to a very large waste while an error in the opposite direction may result in wholesale semi-starvation.

The Maintenance of Constant Weight. The experience of most adults is that during periods of unbroken health the Body weight remains practically unchanged day in and day out. It is clear that this condition depends on the maintenance of an exact balance between the intake and outgo of the Body, since if more is taken in than is given out there must be a gain in weight, and vice versa. It is customary to consider the question of weight maintenance under three heads: *water equilibrium*, *nitrogen equilibrium*, and *carbon equilibrium*.

Water Equilibrium. For a Body to be in water equilibrium the amount of water lost per day must be exactly replaced by the amount drunk. In large measure the sudden and transient changes of weight which occur are due to upsets of water equilibrium. Any violent exercise in hot weather reduces the weight by inducing a

profuse perspiration with resulting loss of water. The intense thirst which follows the exercise leads to abundant ingestion of water and a speedy restoration of the lost weight.

Nitrogen Equilibrium. Those metabolic activities of living tissues which result in tissue breakdown are particularly associated with the use of protein foods, since, as we have seen, their repair can be accomplished only by proteins. The characteristic constituent of protein is nitrogen; and the simplest way to estimate the amount of protein contained in any food mass, or represented by any particular amount of excretion, is to determine the nitrogen and multiply the weight of it present by 6.25, the fraction of protein which is nitrogen. We shall learn in the chapter on Excretion (Chap. XXXI), that in the healthy Body an accumulation of nitrogen-containing excretory products never occurs; as fast as wastes are formed they are got rid of. It follows, then, that if there is less nitrogen being given off than taken in, the living tissues of the Body must be increasing in amount, and if more is given off than is obtained in the food the living tissues must be wasting away. In the healthy adult Body, neither of these conditions is at all usual; the intake and outgo of nitrogen balance each other and the Body is in nitrogen equilibrium.

It has been chiefly through experimental studies of nitrogen equilibrium that our ideas of the twofold function of protein, as tissue-restorer and as fuel, have been gained. If an animal be fed large enough quantities of protein he requires no other food, and if healthy maintains nitrogen equilibrium upon this high level, the large nitrogen intake being exactly balanced by an equally large outgo. Now by substituting other foods, as carbohydrates or fats, for part of the protein, the nitrogen intake and outgo are each less in quantity, but they still balance; the animal is in nitrogen equilibrium upon a lower level. If the substitution of other foods for protein is increased a point is presently reached when the nitrogen outgo exceeds its intake; the animal is not getting enough protein for his needs, and so his own tissues are breaking down (p. 533). During the growth period, on the other hand, or after a wasting illness, when new tissue is being formed, the nitrogen balance is the other way; the amount lost from the Body daily is less than that consumed. The hearty appetites of children and convalescents are associated with this necessity of

taking sufficient nourishment to insure a supply of protein for tissue building.

Carbon Equilibrium. For an animal to be in carbon equilibrium only needs that all the fuel taken in be burned, and that no reserve store be called upon. Aside from the temporary storage of carbohydrate food as glycogen all the fuel taken into the Body must look forward to one of two fates, either to be oxidized promptly or to be stored in the form of fat for future use. Just as nitrogen equilibrium may be established on a high or a low level so carbon equilibrium can be maintained in the face of variations in the intake of fuel. It is easily seen, however, that the limits of carbon equilibrium must be narrower than of nitrogen equilibrium. The actual protein requirement of the Body is so much less than the usual protein intake that considerable variations in the protein consumed can be made without affecting the nitrogen equilibrium; but the energy requirement of the Body is quite definite, varying with the work done rather than with the food eaten. Thus it follows that the fuel intake and the energy requirement are harder to keep balanced than are the nitrogen intake and outgo. It may easily be a matter of astonishment how successfully the Body, under the guidance of the appetite, manages to make its fuel consumption balance its fuel need.

There is a difference of opinion among Physiologists as to whether every accidental excess consumption of fuel results in the normal individual in the deposition of the surplus in the form of fat, or whether the Body has the power to carry on oxidations in excess of the normal basal metabolism and of the amount of muscular exercise.

Such positive information as we have on this point (see next paragraph) is based on observations on abnormal individuals and cannot be taken as necessarily applying to persons in normal health.

The Influence of the Thyroid Hormone upon Metabolism. In a previous chapter (p. 26) the point has been emphasized that the amount of oxidation going on in any tissue in basic metabolism, or in the Body as a whole for that matter, depends on the quantity of hydrogen transporters available. Thyroxin, the hormone of the thyroid gland, we have already seen to be one of the most important of the substances of this class. It follows that whether

excess fuel shall be stored as fat or be burned, depends to a large extent, at least, on the amount of the thyroid hormone produced. When the hormone is abundant the bodily oxidations are so vigorous that no surplus of fuel remains to be converted into fat. An inactive thyroid gland, on the other hand, signifies a likelihood of fat formation whenever the consumption of food happens to exceed the immediate energy requirement. In the disease known as *exophthalmic goiter* (*Graves' Disease*) the thyroid gland is abnormally active. The chief symptoms of the disease are those associated with a greatly augmented metabolism. Sufferers from the condition eat hugely and yet are often emaciated. Measurements of the daily energy turnover show a heat production that may be virtually double that of normal persons.

In the opposite condition, myxedema (p. 216), the oxidations are on less than normal scale, with resultant tendency to lay on weight. It is probable that many persons owe their marked tendency to obesity to a slight hypothyroidism, not sufficient to induce nervous symptoms, but enough to make it likely that more food will be eaten than can be oxidized.

The Treatment for Obesity is obviously to make the energy expenditure equal, or even exceed, the fuel intake. Vigorous muscular exercise accompanied by strict dietary limitation may produce the desired result, but the good effects continue only so long as the flesh-reducing measures are persisted in. Exercise and dieting are both conducive to good appetite, therefore as soon as the treatment is relaxed a return to the former condition is virtually inevitable. Persistent semi-starvation, unaccompanied by active exercise, is an efficient weight reducer. It should be resorted to with intelligence, however, for undesirable impairment of strength may follow its injudicious employment. A good rule for those who wish to avoid gaining flesh is never to satisfy the appetite wholly. On account of its marked specific dynamic action (p. 541) protein is usually made the chief constituent of the diet in the treatment of obesity.

The administration of thyroid extract is a means of reducing flesh by stimulating the oxidation processes of the Body. Since the thyroid hormone has effects upon the nervous system (p. 216) as well as upon general metabolism this treatment should never be undertaken except under competent medical advice.

Source of the Body Fat. For a long time there was much discussion as to which of the three sorts of food stuffs, proteins, carbohydrates, or fats, is the source of the fat which is stored in the Body. The natural conclusion that Body fat is derived from food fat is shown to be not inevitably true, at any rate, by the ability of cattle to produce milk, with its abundant fat content, upon a diet of hay and grain in which no trace of fat occurs. The question whether in these animals the protein or the carbohydrate of the food gives rise to the fat was formerly much studied; but with the rise of the modern view of normal protein metabolism, according to which all but a small percentage of the protein taken in the food is deaminized and used as carbohydrate, the question has lost much of its force. There can be little doubt that Body fat represents stored fuel, and since the whole fuel supply of the bovine Body is often represented by carbohydrates (plus deaminized amino acids), these must be the source of the fat which the Body elaborates.

Even in animals whose diet includes some fat the normal source of the Body fat is usually for the most part carbohydrate. The situation is simply that surplus nutrients tend to be deposited as storage material against a time of future shortage; the capacity of the Body for glycogen is usually nearly all occupied all the time; consequently excess fuel stuffs, either fats or sugars, must be deposited as fats if stored at all, and they are so deposited in proportion to their availability. Since carbohydrates are usually taken more abundantly than fats they ordinarily form a larger proportion of the available surplus.

CHAPTER XXXI

EXCRETION AND THE EXCRETORY ORGANS

Exogenous and Endogenous Excreta. It is usual to include under the general head of *excreta* all waste materials of any kind given out from the Body. We shall see, however, that under this general definition come two very distinct classes of materials. Many substances are taken into the Body with the food which have of themselves no food value, and escape absorption during the passage of the food through the alimentary tract; these appear, of course, among the excreta. Other substances have an accessory food value, in arousing appetite, or in stimulating some of the bodily processes; these may be absorbed from the alimentary tract into the blood, but they do not enter in any intimate fashion into the metabolic activities of the living tissues, and after a longer or shorter sojourn in the blood they appear among the excreta. The third substances to be grouped with those just described are the nitrogen-containing compounds which are split off from the fuel-proteins in the process of deamination. These, from the moment of their separation, are waste products, to be conveyed as rapidly as possible to the excretory organs and got rid of. All these excretory materials are grouped together as *exogenous excreta*, the term suggesting that they are derived from sources outside the actual life processes of the tissues.

The second group of excreta, the *endogenous excreta*, includes substances produced by the living cells of the Body in the course of their metabolic activities. Most of our knowledge of cell metabolism has been gained through studies of the endogenous excreta.

The Channels of Excretion. Four channels are recognized through which the Body discharges waste materials; these are: the *lungs*, the *skin*, the *urinary system*, the *rectum*. The lungs are the channel for the discharge of gaseous wastes, carbon dioxid, and water vapor; the skin eliminates a part of the water and traces of the nitrogenous excreta; the urinary system disposes of the

major part of the endogenous excreta other than gaseous, and also of exogenous excreta absorbed from the alimentary tract into the blood. From the rectum are discharged all exogenous excreta that fail of absorption, and likewise a number of endogenous excretory substances received into the intestine from the liver, by way of the bile duct. The chapter on Respiration contains the discussion of the excretory function of the lungs. It is not necessary, therefore, to consider it here.

The Liver as an Excretory Organ. To the functions previously described of aiding the digestive and absorptive processes, and of serving as a temporary storehouse for carbohydrates, the liver adds a very important excretory function. This is in part direct, the separation from the blood of waste materials contained in it, and in part the working over of harmful excretory substances into harmless ones which it does not excrete but returns to the blood to be discharged through the urinary system and skin. This latter function will be considered before the direct excretions of the liver are discussed. It will be recalled that by the process of deamination (p. 535) the "fuel-protein" is split into a nitrogenous waste portion, and a non-nitrogenous oxidizable portion. The nitrogenous part takes the form largely of ammonia compounds, chief of which is ammonium carbonate $(NH_4)_2CO_3$. This decomposition of amino acids takes place anywhere in the Body where the acids are present in excess of the tissue repair requirements. In the nature of the case it occurs most abundantly in the liver, since that organ is the first to be permeated with blood bearing freshly absorbed amino acids, and furthermore has passing through it all the blood coming from the intestinal tract, where the absorption occurs. Indeed, if it were not that the blood flows so rapidly that there is not time for the liver-cells to take up and deaminize all the amino acids they themselves do not need, none would escape to supply the requirements of the other tissues. As it is considerably more deamination occurs in the liver in proportion to the amount of tissue present, than in other parts of the Body.

The ammonia compounds are highly poisonous if present in the blood in more than minute amounts. They are rendered innocuous, or nearly so, by being promptly converted by dehydration into *urea*, a compound harmless to the Body if not present in the

blood in too great concentration. The conversion of ammonium carbonate by dehydration to urea is made clear if we compare the chemical formulæ of the two substances:

$$CO<\begin{matrix}NH_4O-H_2O\\NH_4O-H_2O\end{matrix}=CO<\begin{matrix}NH_2\\NH_2\end{matrix}$$

(ammonium carbonate) (urea)

This conversion occurs in general wherever in the Body the formation of ammonia occurs. There are a few exceptions to this statement, however. One that interests us at this point is the formation of ammonia in connection with putrefaction processes in the intestine. It is well known that when such processes occur considerable ammonia is produced. This is not changed into urea in the intestinal wall, but is absorbed as such into the blood and conveyed to the liver, where the conversion takes place. This urea-formation, added to that resulting from the dehydration of ammonium carbonate produced in deamination processes in the organ, makes the liver easily the largest source of urea in the Body. So dominant is it, in fact, that for a long time the view was held that all the ammonia compounds produced anywhere in the Body are conveyed to the liver for dehydration. Although we now know it to act only on ammonia produced within itself, and on such as is formed in intestinal putrefaction, it is still proper to assign it a function in preparing excretory products for elimination elsewhere. The urea formed thus from ammonia compounds belongs to the group of exogenous excreta, since it does not represent a product of cell true metabolism in the Body. From the liver it is delivered to the blood of the general circulation where it remains till excreted by the kidneys.

The direct excretory function of the liver consists in the withdrawal from the blood and the delivery to the intestine through the bile of certain endogenous excretory substances. The most marked of these are the *bile-pigments*, which, as stated in Chap. XVII, are derived from the worn-out red corpuscles of the blood, and consist essentially of the pigment portion of hemoglobin minus its iron. Two bile-pigments occur, of very similar chemical constitution; *bilirubin*, golden-brown in color, is the predominating pigment of carnivorous bile, and of human bile on a mixed diet;

biliverdin, a green pigment, predominates in the bile of herbiverous animals.

Beside the bile-pigments the liver excretes small amounts of various substances which are interesting chiefly on account of their insolubility in the ordinary fluids of the Body, and the fact that they are soluble in bile. These are found in minute amounts in all cells; slightly more abundantly in nerve tissues than elsewhere. They are probably true endogenous excreta, set free in the course of metabolism. The most abundant of them is the non-nitrogenous compound *cholesterol*.

The chief constituents of bile not heretofore mentioned are the *bile salts*, sodium salts of peculiar acids found only in bile, *glycocholic acid* and *taurocholic acid*. These do not appear to be excreta in any proper sense of the word, inasmuch as they are reabsorbed virtually in toto by the intestinal walls, and returned by the portal vein to the liver whence they again appear as constituents of the bile. They are thought to give to bile its special ability to promote fat absorption by dissolving the fatty acids, and it is also by virtue of their presence that the bile is able to dissolve cholesterol.

General Arrangement of the Urinary Organs. These consist of (1) the *kidneys*, the organs which secrete the urine; (2) the *ureters* or ducts of the kidneys, which carry their secretion to (3) the *urinary bladder*, a reservoir in which it accumulates and from which it is expelled from time to time through (4) an exit tube, the *urethra*. The general arrangement of these parts, as seen from behind, is represented in Fig. 142. The two kidneys, *R*, lie in the dorsal part of the lumbar region of the abdominal cavity, one on each side of the middle line. Each is a solid mass, with a convex outer and a concave inner border, and its upper end a little larger than the lower. From the abdominal aorta, *A*, a *renal artery*, *Ar*, enters the inner border of each kidney, to break up within it into finer branches, ultimately ending in capillaries. The blood is collected from these into the *renal veins*, *Vr*, one of which leaves each kidney and opens into the inferior vena cava, *Vc*. From the concave border of each kidney proceeds also the *ureter*, *U*, a slender tube from 28 to 34 cm. (11 to 13.5 inches) long, opening below into the bladder, *Vu*, on its dorsal aspect, and near its lower end. From the bladder proceeds the urethra, at *Ua*. The channel of each ureter passes very obliquely through the wall of

the bladder to open into it; accordingly if the pressure inside the latter organ rises above that of the liquid in the ureter, the walls of

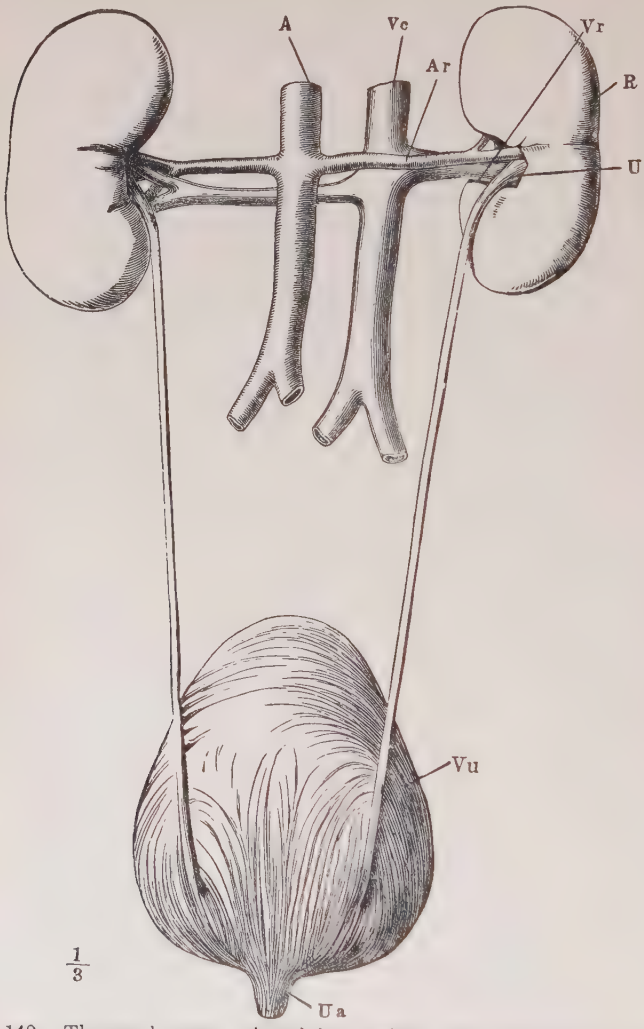


FIG. 142.—The renal organs, viewed from behind. *R*, right kidney; *A*, aorta; *Ar*, right renal artery; *Vc*, inferior vena cava; *Vr*, right renal vein; *U*, right ureter; *Vu*, bladder; *Ua*, commencement of urethra.

the oblique passage are pressed together and it is closed. Usually the bladder, which has a thick coat of smooth muscular tissue

lined by a mucous membrane, is relaxed, and the urine flows readily into it from the ureters. While urine is collecting, the beginning of the urethra is kept closed, in part at least, by bands of elastic tissue around it: some of the muscles which surround the commencement of the urethra assist, being kept in reflex contraction; it is found that in a dog the urinary bladder can retain liquid under considerably higher pressure when the spinal cord is intact than after destruction of its lumbar portion. The contraction of these urethra constricting muscles can be reinforced voluntarily. When some amount of urine has accumulated in the bladder, it contracts and presses on its content; the ureters being closed in the way above indicated, the elastic fibers closing the urethral exit are overcome, and the urethral muscles simultaneously relaxing, the liquid is forced out.

Naked Eye Structure of the Kidneys. These organs have externally a red-brown color, which can be seen through the transparent *capsule* of peritoneum which envelops them. When a section is carried through a kidney from its outer to its inner border (Fig. 143) it is seen that a deep fissure, the *hilus*, leads into the latter. In the *hilus* the ureter widens out to form the *pelvis*, *D*, which breaks up again into a number of smaller divisions, the cups or *calices*. The cut surface of the kidney proper is seen to consist of two distinct parts: an outer or *cortical portion*, and an inner or *medullary*. The medullary portion is less red and more glistening to the eye, is finely striated in a radial direction, and does not consist of one continuous mass but of a number of conical portions, the *pyramids of Malpighi*, 2′, each of which is separated from its neighbors by an inward prolongation, 4, of the cortical substance: this, however, does not reach to the inner end of the pyramid, which projects, as the *papilla*, into a calyx of the ureter. At its outer end each pyramid separates into smaller portions, the *pyramids of Ferrein*, 2″, separated by thin layers of cortex and gradually spreading everywhere into the latter. The cortical substance is redder and more granular looking and less shiny than the medullary, and forms everywhere the outer layer of the organ next its capsule, besides dipping in between the pyramids in the way described.

The renal artery divides in the hilus into branches (5) which run into the kidney between the pyramids, giving off a few twigs

to the latter and ending finally in a much richer vascular network in the cortex. The branches of the renal vein have a similar course.

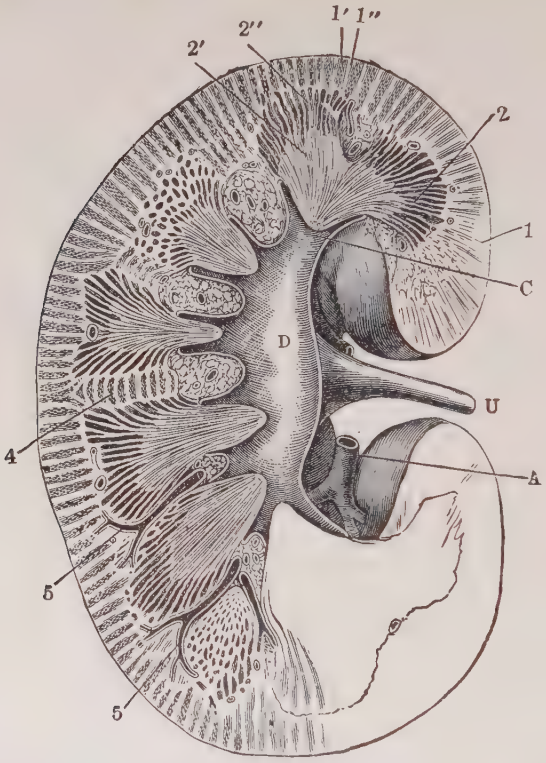


Fig. 143.—Section through the right kidney from its outer to its inner border, 1, cortex; 2, medulla; 2′, pyramid of Malpighi; 2″, pyramid of Ferrein; 5, small branches of the renal artery entering between the pyramids; *A*, a branch of the renal artery; *D*, the pelvis of the kidney; *U*, ureter; *C*, a calyx.

The Minute Structure of the Kidney. The kidneys are compound tubular glands, composed essentially of branched microscopic *uriniferous tubules*, lined by epithelium. Each tubule commences at a small opening on a papilla and from thence has a very complex course to its other extremity: usually about twenty open, side by side, on one papilla, where they have a diameter of about 0.125 mm. ($\frac{1}{200}$ inch). Running from this place into the pyramid each tubule divides repeatedly; the ultimate branches, which are the secreting tubules, pursue a tortuous course (Fig. 144)

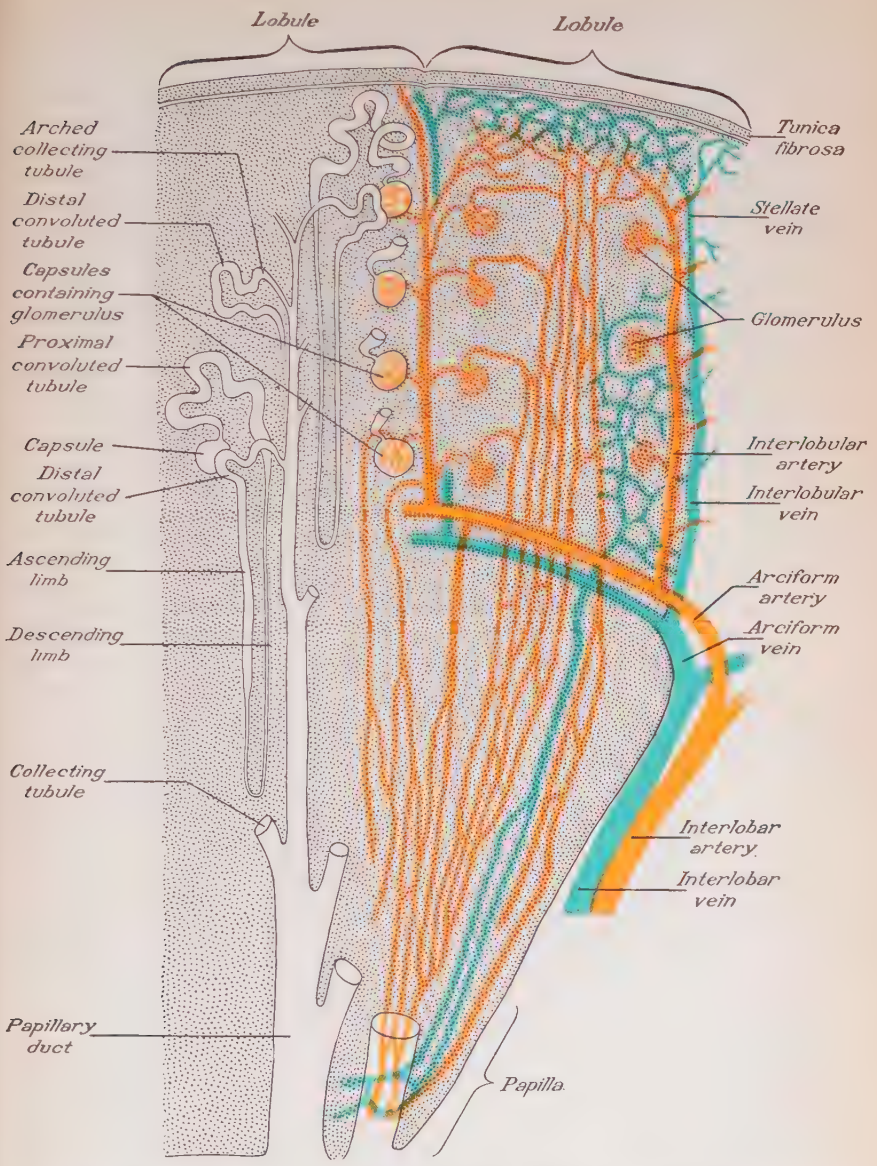


FIG. 144.—Diagram of kidney tubule and renal blood-vessels (Lewis and Stöhr).

to terminations in the cortex of the kidney in peculiar spherical dilatations, the *Malpighian capsules*, each containing a tuft of capillaries, the *glomerulus* (Fig. 145). Throughout its course the tubule is lined by a single layer of epithelium cells differing in character in its different sections: they are flat and clear in the capsules, and very granular in the convoluted parts, where their appearance suggests that they are not mere lining cells but cells with active work to do; in the collecting and discharging tubules they are somewhat cuboidal in form and do not appear to have an active secretory function. All the tubes are bound together by a sparse amount of connective tissue and by blood vessels to form the entire organ. The lymph-spaces are large and numerous, especially about the convoluted portions of the tubules.

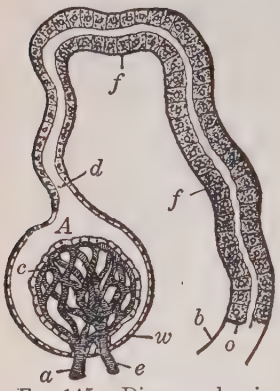


FIG. 145.—Diagram showing a kidney glomerulus and the commencement of an uriniferous tubule. *a*, afferent blood-vessel pushing in the wall, *w*, of a Malpighian capsule and ending in the capillary tuft from which the vein *e* issues; *c*, involuted epithelium covering the vascular tuft; for the sake of distinctness it is represented as a general wrapping for the whole tuft, but in nature it forms a close investment around each vessel of the glomerulus; *A*, space in capsule into which liquid transuded from the vessels of the glomerulus passes; *d*, neck of capsule passing into commencement of first convoluted portion, *f f*, of an uriniferous tubule; *o*, granular epithelial cells; *b*, basement membrane.

The Blood-Flow Through the Kidney. The amount of blood brought to the kidney is large relatively to the size of the organ and enters under a very high pressure almost direct from the aorta, and leaves under a very low, into the inferior cava (Fig. 142). The final twigs of the renal artery in the cortex, giving off a few branches which end in a capillary network around the convoluted tubules and in the pyramids, are continued as the *afferent vessels* of Malpighian capsules, the walls of which are doubled in before them (Fig. 145); there each breaks up into a little knot of capillary vessels called the *glomerulus*, from which ultimately an *efferent vessel* proceeds. Where the wall of the capsule, *w*, Fig. 145, is doubled in before the blood vessels, its lining cells continue as a covering, *c*, to the latter, closely adhering to the vascular walls. A space, *A*, is left between the epithelial cells of the outside of the capsule and those involuted on the vessels, as there would be in the interior

of a rubber ball one side of which was pushed in so as to nearly meet the other; this cleft, into which any liquid transuded from the vessels must enter, opens by a narrow *neck*, *d*, into the commencement of the first contorted part of an uriniferous tubule. The efferent vein, carrying blood away from the glomerulus, breaks up into a close capillary network around the neighboring tubules of the cortex (Fig. 144). From these capillaries the blood is collected into the renal vein. Most of the blood flowing through the kidney thus goes through two sets of capillaries; one found in the capsules, and the second formed by the breaking up of their efferent veins. The capillary network in the pyramids is much less close than that in the cortex, which gives reason to suspect that most of the secretory work of the kidneys is done in the capsules and convoluted tubules. The pyramidal blood flows only through one set of capillaries, there being no glomeruli in the kidney medulla.

The Renal Excretion. The amount of this carried off from the Body in 24 hours is subject to considerable variation, being especially diminished by anything which promotes perspiration, and increased by conditions, as cold to the surface, which diminish the skin excretion. Its average daily quantity varies from 1,200 to 1,750 c. c. (40 to 60 fluid ounces). The urine is a clear amber-colored liquid, usually of a slightly acid reaction; its specific gravity is about 1.022, being higher when the total quantity excreted is small than when it is greater, since the amount of solids dissolved in it remains nearly the same in health; the changes in its bulk being dependent mainly on changes in the amount of water separated from the blood by the kidneys.

Normal Urine consists of about 96 per cent water and 4 per cent dissolved solids. Chemically it is a very complex liquid, the 4 per cent of dissolved materials including a large variety of different substances. This is to be expected when we recall that the kidney is the excretory channel, not only for the chief part of the endogenous excreta, but also for virtually all the exogenous waste materials that are absorbed into the blood-stream. Among these latter are found the substances that lend flavor to our food; likewise most drugs that are taken find their way ultimately into the urine. One group of exogenous urinary substances, the *ethereal sulphates*, are interesting since they are derived from compounds formed in the large intestine in the course of the putrefactive

processes which normally go on there; these compounds are absorbed into the blood-stream and are excreted by the kidney. The extent of their occurrence in the urine measures the amount of putrefaction in the large intestine. These substances are toxic if present in quantity and the ill feeling which accompanies true autointoxication (p. 507) is the result of their presence in considerable concentration in the blood.

Urea is the constituent of urine most abundant next to the water. About two per cent of urine, half of all the dissolved materials, is urea. The greater part of this is of exogenous origin, being formed in the liver from the ammonia residues of fuel-protein. The amount of exogenous urea varies from time to time according as the amount of protein undergoing absorption varies. It is thought that a certain amount of endogenous urea is produced during the course of cell metabolism. How much of the total urea of the excretion is of this origin cannot be told.

Creatinine. In some respects the most interesting of the endogenous excreta found in the urine is the compound *creatinine.* The daily elimination of this substance, as stated in Chap. I, is practically constant for a given individual, and appears to be determined chiefly by the amount of muscle-tissue present in the Body. If its output is followed moment by moment, however, it is found to rise during muscular exercise and to fall correspondingly after the exercise is over. The extent of drop is greater the greater the rise due to the exercise, so that even though the amount or vigor of the latter varies greatly from day to day, the elimination of creatinine for the day as a whole comes out constant. The precise significance of this waste-product is unknown. Measurements of its daily quantity are useful as clues to the general muscular make-up and potential muscular ability of individuals.

The Purin Bodies, of which uric acid is the best known, are other endogenous excreta found in urine. They show chemical characteristics which indicate that they represent probably the end products of the metabolism of cell nuclei. Caffein, the active principle of coffee and tea, and theobromin, the active principle of cocoa, are very closely related chemically to the purin bodies excreted from the kidney.

Since all the endogenous excreta are produced in the living tissues they occur in the flesh of animals eaten for food. In fact

the flavor of meat is largely the result of their presence. When eaten with meat they are, of course, absorbed into the blood from the intestine and become part of the exogenous excreta. For this reason it is often necessary, when studying metabolism experimentally, to exclude meat from the diet, so that the endogenous excreta may be obtained pure.

The Urinary Salts are chiefly sodium chlorid, and the sulphates and acid phosphates of sodium, potassium, calcium, and magnesium. Whatever salt is taken with the food, unless stored permanently in the Body, as in bone formation, finally is excreted by the kidneys. The acid phosphates of sodium and potassium are in part responsible for the acid reaction of urine.

In various diseases abnormal substances are found in the urine: the more important are albumens in *albuminuria* or *nephritis;* glucose in *diabetes;* bile salts; bile pigments.

The Actions of Different Parts of an Uriniferous Tubule. The microscopic structure of the kidneys is such as to suggest that in those organs we have to do with two essentially distinct apparatuses: one represented by the glomeruli, with their capillaries separated only by a single layer of flat epithelial cells from the cavity of the capsule and especially adapted for filtration; the other represented by the contorted portions of the tubules, with their large granular cells, which clearly have some more active part to play than that of a mere passive transudation membrane. And we find in the urine substances which like the water and mineral salts may easily be accounted for by mere physical processes, and others, urea especially, which are present in such proportion as must be due to some active physiological work of the kidney. More direct evidence does, in fact, justify us in saying that in general the glomeruli are transudation organs, the contorted portions of the tubuli secretory organs, while the collecting and discharging tubules are mainly passive channels for the gathering and transmission of liquid.

Function of the Glomeruli. These structures, as indicated above, are simple filters. Their delicate membranous walls must be pictured as possessing ultramicroscopic pores; pores so inconceivably minute, in fact, that only molecules smaller than protein molecules can pass through them. As the blood flows through the glomerular capillaries it is under pressure (see below); consequently

water filters through the glomerular walls, together with all the sorts of molecules dissolved in it except those too large to pass through the openings, which molecules are left behind in the blood-plasma. The filtrate appearing in the upper end of the tubule (at *d*, Fig. 145) is therefore identical in composition with blood-plasma, except that the large molecules (relatively speaking) present in the latter are absent from the filtrate. The amount of filtrate formed per unit of time depends on the *effective* pressure of the blood in the glomerular capillaries. This effective pressure is less than the hydrostatic pressure because the large molecules dissolved in blood-plasma, but not present in the filtrate, exert a small osmotic pressure (p. 32) tending to cause water to flow *backward* from filtrate to blood; to counteract this an equivalent hydrostatic pressure in the opposite direction must be maintained. It follows that an actual flow of water can be caused only by a still greater hydrostatic pressure, and it is this excess hydrostatic pressure that constitutes the effective pressure causing filtration. The best estimates we have indicate that the osmotic pressure to be overcome in forming glomerular filtrate is equivalent to about 30 mm. Hg., and the average hydrostatic pressure, about 90 mm. Hg., giving an effective filtration pressure of about 60 mm. Hg.

Various methods have been devised for getting samples of glomerular filtrate for comparison with finished urine; lack of space forbids their description here. By their use it has been pretty conclusively shown that the filtrate answers the description given above, *i. e.*, that of blood-plasma, minus certain large molecules. They have also indicated that under ordinary conditions the *bulk of filtrate* formed per unit of time is perhaps between two and ten times as large as of the urine emerging from the outlets of the tubules into the pelvis of the kidney. This shows that by some means the volume of fluid becomes considerably reduced during the flow of the same along the tubules. Comparison of the composition of urine with that of blood-plasma shows, furthermore, that some substances present in the latter are absent from the former (sugar and amino acids chiefly), and that most of the substances found in both are in very different concentrations in the two.

Functions of the Convoluted Tubules. Evidently the changes described above are brought about by the "secretory" cells of the

convoluted tubules during the passage of the glomerular filtrate along the latter. Water is reduced in amount and sugar and amino acids ordinarily disappear altogether; only one explanation is possible, *i. e.*, that the tubule cells *reabsorb* these substances; sugar and amino acids completely (or virtually so; traces of both are usually present in urine); water to the extent of 50–90 per cent ordinarily. The substances present in urine in more than ten times their concentration in plasma (urea, uric acid, phosphates, and sulphates, chiefly) must be actively secreted by the cells of the convoluted tubules. In some of the lower forms, as frogs, sodium chlorid is like sugar in that it is almost completely reabsorbed. In man and the higher animals generally it is reabsorbed to some extent, but not completely; this difference is associated with the fact that in the latter sodium chlorid is regularly ingested, thus balancing the loss in the urine, and keeping the salt content of the Body uniform.

Threshold Substances. The substances that enter the urine only by filtration through the glomerular membranes must obviously occur in the *glomerular filtrate* in precisely the same proportion as in blood-plasma; whenever the concentration of such substances in the blood rises, their concentration in the glomerular filtrate increases in exact correspondence. If the substances whose concentration rises are reabsorbed by the cells of the convoluted tubules (sugar for example), it is obvious that reabsorption must become more active as the concentration rises, and in proportion to the increase in concentration, otherwise some of the material will escape reabsorption, and appear in the urine. This is precisely what happens in the case of sugar. The tubule cells can reabsorb all that comes to them up to a concentration of about 0.17 per cent, but when the blood-plasma, and consequently the glomerular filtrate, reaches a higher concentration than that (as in diabetes, p. 528) some of the surplus escapes reabsorption and appears in the urine. Thus the condition of glycosuria (p. 524) comes about. Any substance that is reabsorbed thus up to some critical concentration is known as a *threshold substance*. Sugar and sodium chlorid are the best examples in our blood. Sugar, as we have just seen, has a threshold somewhat above its normal concentration in plasma, consequently it is all ordinarily reabsorbed. The threshold for sodium chlorid, on the other hand,

is lower in man and mammals than its normal concentration in plasma, and some of it accordingly appears regularly in urine.

The Relation of Renal Blood-Flow to the Secretion of Urine. The kidneys have probably a richer blood supply than any other organs of the Body. It has been estimated that under proper circumstances their own weight of blood may flow through them each minute. This rich blood supply is, of course, an adaptation to secure the withdrawal of waste substances from the blood at a rapid rate. From the structure of the glomeruli and the fact that most of the water of the urine is derived from them it is *a priori* probable that anything tending to increase the pressure of blood in them will increase the bulk of urine secreted, and anything diminishing that pressure will decrease the urine. The structure of the glomeruli themselves is such that the pressure of blood with them tends to be higher than in the capillaries in general. Reference to Figure 145 shows that the vessel which drains the glomerulus, the efferent vessel *e*, is smaller than the afferent vessel *a*. This means that there is a resistance to the outflow from the capsule greater than that at the point of entrance. According to the relation between pressure and resistance (p. 380) there must be a correspondingly greater pressure in the glomeruli than in the other capillaries whose outlet is not similarly restricted. This high glomerular pressure favors filtration. Experiment shows, moreover, that the vigor of urine formation depends on the pressure of blood within the capsule. The kidney is supplied with both vasoconstrictor and vasodilator nerves which reach it mainly through the solar plexus. When the spinal cord is cut in the neck region of a dog the kidney vessels as well as those of the rest of its Body dilate and blood-pressure everywhere is very low. Under these circumstances the secretion of urine is suppressed. If the lower end of the cut cord be stimulated the vessels all over the Body of the animal contract, and blood-pressure everywhere becomes very high. But the kidney vessels being constricted with the rest allow very little blood to enter the glomeruli in spite of the high aortic pressure, and little or no urine is secreted. If, however, the vasoconstrictor nerves of the kidney be cut before the stimulation of the cord, we get a dilation of the kidney vessels with a constriction of vessels elsewhere, and abundant blood flows through the glomeruli under high pressure: the whole kidney swells and abun-

dant urine is formed. When the skin vessels contract on exposure to cold, more blood flows through internal organs, the kidneys included, and the blood-pressure in these is if anything increased. Hence the greater secretion of urine in cold weather.

In addition to these changes in circulation affecting the whole kidney there are local changes of great importance. It has been shown recently (by direct observation of living frogs' kidneys under the microscope) that individual glomeruli open and close from time to time, so that they may function for a while, and then as the result of constriction of the capillaries within them may become wholly inactive for a time. In a kidney functioning at the rate observed in an ordinarily quiet body about one in five of the glomeruli may be open; the tubules connected with these open glomeruli are obviously the only ones forming urine. It follows that only a fraction of the potential capacity of the kidney is needed for the successful elimination of the accumulated wastes under ordinary conditions. In the next paragraph something is said as to situations which may bring about variation in the number of open glomeruli.

Diuretics. Various substances, caffein, digitalis, urea, salts, and even water, bring about increased formation of urine; the condition is known as *diuresis*, and the substances which cause it as *diuretics*. These may act by causing vasodilation in the kidney vessels (particularly the *afferent* vessels of the glomeruli), or by causing glomeruli previously closed to open out, or possibly in some cases by affecting the reabsorptive power of the cells of the convoluted tubules. The effect of such a substance as caffein to cause glomeruli previously closed to open out is very striking as seen under the microscope. An opposite action, closing of previously open glomeruli, may be induced by adrenin or pituitrin (p. 400) in suitable doses.

The Skin, which covers the whole exterior of the Body, consists everywhere of two distinct layers; an outer, the *cuticle* or *epidermis*, and a deeper, the *dermis*, *cutis vera*, or *corium*. A blister is due to the accumulation of liquid between these two layers. The *hairs* and *nails* are excessively developed parts of the epidermis.

The Epidermis, Fig. 146, consists of cells, arranged in many layers, and united by a small amount of cementing substance. The deepest layer, *d*, is composed of elongated or columnar cells,

set with their long axes perpendicular to the corium beneath. To it succeed several layers of roundish cells, *b;* in more external layers the cells become more and more flattened in a plane parallel to the surface. The outermost epidermic stratum is composed of

Fig. 146.—A section through the epidermis, somewhat diagrammatic, highly magnified. Below is seen a papilla of the dermis, with its artery, *f*, and veins, *g g; a*, the horny layer of the epidermis; *b*, the *rete mucosum* or Malpighian layer; *d*, the layer of columnar epidermic cells in immediate contact with the dermis; *h*, the duct of a sweat-gland.

many layers of extremely flattened cells from which the nuclei (conspicuous in the deeper layers) have disappeared. These superficial cells are dead and are constantly being shed from the surface of the Body, while their place is taken by new cells, formed in the deeper layers, and pushed up to the surface and flattened

in their progress. The change in the form of the cells as they travel outwards is accompanied by chemical changes, and they finally constitute a semitransparent dry *horny stratum*, *a*, distinct from the deeper, more opaque and softer *Malpighian* or *mucous layer*, *b* and *d*, of the epidermis.

The rolls of material which are peeled off the skin in the "shampooing" of the Turkish bath, or by rubbing with a rough towel after an ordinary warm bath, are the dead outer scales of the horny stratum of the epidermis.

In dark races the color of the skin depends mainly on minute *pigment-granules* lying in the cells of the deeper part of the Malpighian layer.

No blood or lymphatic vessels enter the epidermis, which is entirely nourished by matters derived from the subjacent corium.

The Corium, Dermis or True Skin, Fig. 147, consists fundamentally of a close feltwork of elastic and white fibrous tissue, which, becoming wider meshed below, passes gradually into the *subcutaneous areolar tissue* (Chap. IV) which attaches the skin loosely to parts beneath. In tanning it is the *dermis* which is turned into leather, its white fibrous tissue forming an insoluble and tough mass as the result of treatment with the tannin of the oak-bark employed.

Wherever there are hairs, bundles of smooth muscular tissue are found in the corium; it contains also a close capillary network and numerous lymphatics and nerves. In shaving, so long as the razor keeps in the epidermis there is no bleeding; but a deeper cut shows at once the vascularity of the true skin.

The outer surface of the corium is almost everywhere raised into minute elevations, called the *papillæ*, on which the epidermis is molded, so that its deep side presents pits corresponding to the projections of the dermis. In Fig. 146 is shown a papilla of the *corium* containing a knot of blood vessels, supplied by the small artery, *f*, and having the blood carried off from them by the two little veins, *g g*. Other papillæ contain no capillary loops but special organs connected with nerve-fibers, and concerned in the cutaneous senses (Chap. XIII). On the palmar surface of the hand the dermic papillæ are especially well developed (as they are in most parts where the sense of touch is acute) and are frequently *compound*, or branched at the tip. On the front of the hand, they

are arranged in rows; the epidermis fills up the hollows between the papillæ of the same row, but dips down between adjacent rows, and thus are produced the finer ridges seen on the palms. In many places the corium is also furrowed, as opposite the finger-joints and on the palm. Elsewhere such furrows are less marked, but they exist over the whole skin. The epidermis closely follows all the hollows, and thus they are made visible from the surface.

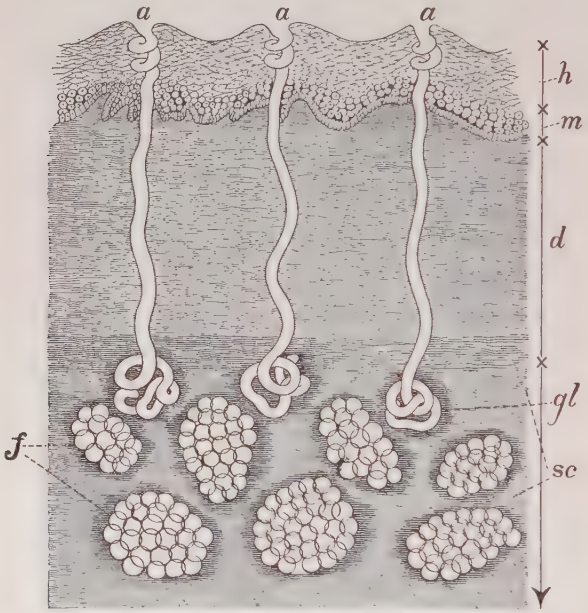


FIG. 147.—A section through the skin and subcutaneous areolar tissue. *h*, horny stratum, and *m*, deeper more opaque layer of the epidermis; *d*, dermis passing below into *sc*, loose areolar tissue, with fat, *f*, in its meshes; above, dermic papillæ are seen, projecting into the epidermis which is molded on them. *a*, opening of a sweat-gland; *gl*, the gland itself.

The wrinkles of old persons are due to the absorption of subcutaneous fat and of other soft parts beneath the skin, which, not shrinking itself at the same rate, is thrown into folds.

Hairs. Each hair is a long filament of epidermis developed on the top of a special dermic papilla, seated at the bottom of a depression reaching down from the skin into the tissue beneath, and called the *hair-follicle*. The portion of a hair buried in the skin is called its *root;* this is succeeded by a *stem* which, in an uncut hair,

tapers off to a *point*. The stem is covered by a single layer of overlapping scales forming the *hair-cuticle;* the projecting edges of these scales are directed towards the top of the hair. Beneath the hair-cuticle comes the *cortex*, made up of greatly elongated cells united to form fibers; and in the center of the shaft there is found, in many hairs, a *medulla*, made up of more or less rounded cells. The color of hair is mainly dependent upon pigment-granules lying between the fibers of the cortex. All hairs contain some air cavities, especially in the medulla. They are very abundant in white hairs and cause the whiteness by reflecting all the incident light, just as a liquid beaten into fine foam looks white because of the light reflected from the walls of all the little air cavities in it. In dark hairs the air cavities are few.

The hair-follicle (Fig. 148) is a narrow pit of the dermis, projecting down into the subcutaneous areolar tissue, and lined by an involution of the epidermis. At the bottom of the follicle is a papilla, and the epidermis, turning up over this, becomes continuous with the hair. On the papilla epidermic cells multiply rapidly so long as the hair is growing, and the whole hair is there made up of roundish cells. As these are pushed up by fresh ones formed beneath them, the outermost layers become flattened and form the hair-cuticle; several succeeding layers elongate and form the cortex; while, in hairs with a medulla, the middle cells retain pretty much their original form and size. Pulled apart by the elongating cortical cells, these central ones then form the medulla with its air-cavities. The innermost layer of the epidermis lining the follicle, has its cells projecting, with overlapping edges turned downwards. Accordingly these interlock with the upward directed edges of the cells of the hair-cuticle; consequently when a hair is pulled out the epidermic lining of the follicle is usually brought with it. So long as the dermic papilla is left intact a new hair will be formed, but not otherwise. Slender bundles of smooth

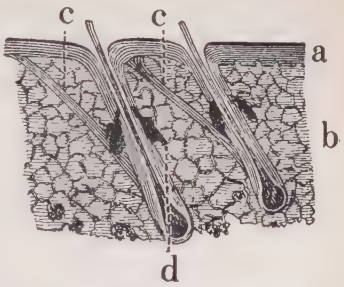


FIG. 148.—Parts of two hairs embedded in their follicles. *a*, the skin, which is seen to dip down and line the follicle; *b*, the subcutaneous tissue; *c*, the muscles of the hair-follicle, which by their contraction can erect the hair; *d*, sebaceous gland.

muscle (*c*, Fig. 148) run from the dermis to the side of the hair-follicles. The latter are in most regions obliquely implanted in the skin so that the hairs lie down on the surface of the Body, and the muscles are so fixed that when they shorten, they erect the hair and cause it to bristle, as may be seen in an angry cat, or sometimes in a greatly terrified man. Opening into each hair-follicle are usually a couple of sebaceous or oil-glands. Hairs are found all over the skin except on the palms of the hands and the soles of the feet; the back of the last phalanx of the fingers and toes, the upper eyelids, and one or two other regions.

Nails. Each nail is a part of the epidermis, with its horny stratum greatly developed. The back part of the nail fits behind into a furrow of the dermis and is called its *root*. The visible part consists of a *body*, fixed to the dermis beneath (which forms the *bed of the nail*), and of a *free edge*. Near the root is a little area whiter than the rest of the nail and called the *lunula*. The whiteness is due in part to the nail being really more opaque there and partly to the fact that its bed, which seen through the nail causes its pink color, is in this region less vascular.

The portion of the corium on which the nail is formed is called its *matrix*. Posteriorly this forms a furrow lodging the root, and it is by new cells added on there that the nail grows in length. The part of the matrix lying beneath the body of the nail, and called its *bed*, is highly vascular and raised up into papillæ which, except in the region of the *lunula*, are arranged in longitudinal rows, slightly diverging as they run towards the tip of the finger or toe. It is by new cells formed on its bed and added to its under surface that the nail grows in thickness, as it is pushed forward by the new growth in length at its root. The free end of a nail is therefore its thickest part. If a nail is "cast" in consequence of an injury, or torn off, a new one is produced, provided the matrix is left.

The Glands of the Skin are of two kinds, the sudoriparous or *sweat-glands*, and the *sebaceous* or *oil-glands*. The former belong to the tubular, the latter to the racemose type. The *sweat-glands*, Fig. 149, lie in the subcutaneous tissue, where they form little globular masses composed of a coiled tube. From the coil a duct (sometimes double) leads to the surface, being usually spirally twisted as it passes through the epidermis. The secreting part of the gland consists of a connective-tissue tube, continuous along

the duct with the dermis; within this is a basement membrane; and the final secretory lining consists of several layers of gland-cells. A close capillary network intertwines with the coils of the gland. Sweat-glands are found on all regions of the skin, but more closely set in some places, as the palms of the hands and on the brow, than elsewhere: there are altogether about two and a half millions of them opening on the surface of the Body.

FIG. 149.—A sweat-gland. *a*, horny layer of cuticle; *c*, Malpighian layer; *b*, dermis. The coils of the gland proper, embedded in the subcutaneous fat, are seen below the dermis.

The *sebaceous glands* nearly always open into hair-follicles, and are found wherever there are hairs. Each consists of a duct opening near the mouth of a hair-follicle and branching at its other end: the final branches lead into globular secreting saccules, which, like the ducts, are lined with epithelium. In the saccules the substance of the cells becomes charged with oil-drops, the protoplasm disappearing; and finally the whole cell falls to pieces, its detritus constituting the secretion. New cells are, meanwhile, formed to take the place of those destroyed. Usually two glands are connected with each hair-follicle, but there may be three or only one. A pair of sebaceous glands are represented on the sides of each of the hair-follicles in Fig. 148.

The Skin Secretions. The skin besides forming a protective covering and serving as a sense organ (Chap. XIII) also plays an important part in regulating the temperature of the Body, and a less important function as an excretory organ, in carrying off water and traces of other waste products.

The sweat poured out by the sudoriparous glands is a transparent colorless liquid, with a peculiar odor, varying in different races and, in the same individual, in different regions of the Body. Its quantity in twenty-four hours is subject to great variations, but usually lies between 700 and 2,000 grams (10,850 and 31,000 grains). The amount is influenced mainly by the surrounding temperature, being greater when this is high; but it is also increased by other things tending to raise the temperature of the Body, as muscular exercise. The sweat may or may not evaporate

as fast as it is secreted; in the former case it is known as *insensible*, in the latter as *sensible perspiration*. By far the most passes off in the insensible form, drops of sweat only accumulating when the secretion is very profuse, or the surrounding atmosphere so humid that it does not readily take up more moisture. The perspiration is acid, and in 1,000 parts contains 990 of water to 10 of solids. Among the latter are found urea (1.5 in 1,000), fatty acids, sodium chlorid, and other salts.

The Nervous and Circulatory Factors in the Sweat Secretion. It used to be believed that an increased flow of blood through the skin would suffice of itself to cause increased perspiration; but against this view are the facts that, in terror for example, there may be profuse sweating with a cold pallid skin; and that in many febrile states the skin may be hot and its vessels full of blood, and yet there may be no sweating.

Direct experiment shows that the secretory activity of the sweat-glands is under immediate control of nerve-fibers, and is only indirectly dependent on the blood-supply in their neighborhood. Stimulating the sciatic nerve of the freshly amputated leg of a cat will cause the balls of its feet to sweat, although there is no blood flowing through the limb. On the other hand, if the sciatic nerve be cut so as to paralyze it, in a living animal, the skin arteries dilate and the foot gets more blood and becomes warmer; but it does not sweat. The *sweat-fibers* doubtless communicate with *sweat-centers* in the medulla, which may either be directly excited by blood of a higher temperature than usual flowing through them or, reflexly, by warmth acting on the exterior of the Body and stimulating the sensory nerves there. Both of these agencies commonly also excite the vasodilator nerves of the sweating part, and so the increased blood-supply goes along with the secretion; but the two phenomena are fundamentally independent. Since the sweat-glands are innervated through the autonomic system they share in the emotional reactions which are characteristic of this system. The effect of embarrassment to cause profuse sweating is too well known to require comment.

The Sebaceous Secretion. This is oily, semifluid, and of a special odor. It contains about 50 per cent of fats (olein and palmatin). It lubricates the hairs and usually renders them glossy. No doubt, too, it gets spread more or less over the skin

and makes the cuticle less permeable by water. Water poured on a healthy skin does not wet it readily but runs off it, as "off a duck's back" though to a less marked degree.

Hygiene of the Skin. The sebaceous secretion, and the solid residue left by evaporating sweat, constantly form a solid film over the skin, which must tend to choke the mouths of the sweat-glands (the so-called "pores" of the skin) and impede their activity. Hence the value to health of keeping the skin clean: a daily bath should be taken by every one.

Bathing. The general subject of bathing may be considered here. One object of it is that above mentioned—to cleanse the skin; but it is also useful to strengthen and invigorate the whole frame. For strong healthy persons a cold bath is the best, except in extremely severe weather, when the temperature of the water may be raised to 15° C. (about 60° F.), at which it still feels quite cold to the surface. The first effect of a cold bath is to contract all the skin-vessels and make the surface pallid. This is soon followed by a reaction, in which the skin becomes red and congested, and a glow of warmth is felt in it. The proper time to come out is while this reaction lasts, and after emersion it should be promoted by a good rub. If the stay in the cold water be too prolonged the state of reaction passes off, the skin becomes cold and pale and the person feels chilly, uncomfortable, and depressed all day. Then bathing is injurious instead of beneficial; it lowers instead of stimulating the activities of the Body. How long a stay in the cold water may be made with benefit depends greatly on the individual: a vigorous man can set up a healthy reaction after much longer immersion than a feeble one; moreover, being used to cold bathing renders a longer stay safe, and, of course, the temperature of the water has a great influence: water called "cold" may vary within very wide limits of temperature, as indicated by the thermometer; and the colder it is the shorter is the time which it is wise to remain in it.

It is perfectly safe to enter a cold bath when warm, and also, when in vigorous health even when feeling chilly, but not when in a depressed vital condition. It is not wise to take a bath immediately after a meal, since the afterglow tends to draw away too much blood from the digestive organs, which are then actively at work. The best time for a long bath is about three hours after

breakfast; but for an ordinary daily dip, lasting but a short time, there is no better period than on rising and while still warm from bed.

The shower-bath abstracts less heat from the skin than an ordinary cold bath and, at the same time, gives it a greater stimulus: hence it has certain advantages.

Persons in feeble health may diminish the shock to the system by raising the temperature of the water they bathe in up to any point at which it still feels cool to the skin. The hot bath is useful as the most efficient means for cleansing the skin and has a distinctly soothing and relaxing influence, of great value to the nervous or over-tired. There is no doubt, however, that its effect tends to be enervating, and it should not be indulged in too frequently.

CHAPTER XXXII

THE PRODUCTION AND REGULATION OF THE HEAT OF THE BODY

Cold- and Warm-Blooded Animals. All animals, so long as they are alive, are the seat of chemical changes by which heat is liberated; hence all tend to be somewhat warmer than their ordinary surroundings, though the difference may not be noticeable unless the heat production is considerable. A frog or a fish is a little hotter than the air or water in which it lives, but not much; the little heat that it produces is lost, by radiation or conduction, almost at once. Hence such animals have no proper temperature of their own; on a warm day they are warm, on a cold day cold, and are accordingly known as *changeable-temperatured* (*poikilothermous*) or, in ordinary language, "cold-blooded" animals. Man and other mammals, as well as birds, on the contrary, are the seat of very active chemical changes by which much heat is produced, and so maintain a tolerably uniform temperature of their own, much as a fire does whether it be burning in a warm or a cold room; the heat-production during any given time balancing the loss, a normal Body temperature is maintained, and usually one considerably higher than that of the medium in which they live; such animals are commonly named "warm-blooded." This name, however, does not properly express the facts; a lizard basking in the sun on a warm summer's day may be quite as hot as a man usually is; but on the cold day the lizard becomes cold, while the average temperature of the healthy Human Body is, within a degree, the same in winter or summer; within the arctic circle or on the equator. Hence it is better to call such animals "*homothermous*" or of uniform temperature.

Moderate warmth accelerates protoplasmic activity; compare a frog dormant in the winter with the same animal active in the warm months: what is true of the whole frog is true of each of its living cells. Its muscles contract more rapidly when warmed, and the white corpuscles of its blood when heated up to the temperature of the Human Body are seen (with the microscope) to

exhibit much more active amœboid movements than they do at the temperature of frog's blood. In summer a frog or other cold-blooded animal uses much more oxygen and evolves much more carbon dioxid than in winter, as shown not only by direct measurements of its gaseous exchanges, but by the fact that in winter a frog can live a long time after its lungs have been removed (being able to breathe sufficiently through its moist skin), while in warm weather it dies of asphyxia very soon after the same loss. The warmer weather puts its tissues in a more active state; and so the amount of work the animal does, and therefore the amount of oxygen it needs, depend to a great extent upon the temperature of the medium in which it is living. With the warm-blooded animal the reverse is the case. Within very wide limits of exposure to heat or cold it maintains its temperature at that at which its tissues live best; accordingly in cold weather it uses more oxygen and sets free more carbon dioxid, thus by its more active internal combustion compensating for its greater loss of heat to the exterior. And it does not become warmer in warm weather, partly because its oxidations are less than in cold (other things being equal), and partly because of physiological arrangements by which it loses heat faster from its body. In fact the living tissues of a man may be compared to hothouse plants, living in an artificially maintained temperature; but they differ from the plants in the fact that they themselves are the seats of the combustions by which the temperature is kept up. Since, within wide limits, the Human Body retains the same temperature no matter whether it be in cold or warm surroundings, it is clear that it must possess an accurate arrangement for heat regulation; either by controlling the production of heat in it, or the loss of heat from it, or both.

The Temperature of the Body. The parts of the Body are all either in contact with one another directly, or, if not, at least indirectly through the blood, which, flowing from part to part, carries heat from warmer to colder regions. Thus, although at one time one group of muscles may work, liberating heat, and at other times another, or the muscles may be at rest and the glands the seat of active oxidation, the temperature of the whole Body is kept pretty much the same. The skin, however, which is in direct contact with external bodies, usually colder than itself, is cooler than the internal organs; its temperature in health

ranges from 20° C. (68° F.) or even lower on the soles of the feet when chilled by contact with an icy pavement to 37° C. (98.5° F.), in the most protected parts, as the hollow of the armpit. In internal organs, as the liver and brain, the temperature is slightly higher than the skin maximum. In the lungs there is loss of the heat carried out by the expired air and that used up in evaporating the water carried out in the breath, so the blood returned to the heart by the pulmonary veins is slightly colder than that carried from the right side of the heart to the lungs.

The Sources of Animal Heat. Apart from heat received from its surroundings and in hot food and drink, the source of heat in the Body is the oxidation of fuel. The 1,750 Calories which represent the basal metabolism (p. 537) all appear as heat; whenever muscular work is done there is an additional by-product of heat. The specific dynamic action of the nutrients results in some additional heat-production while they are being absorbed (p. 541).

The Maintenance of a Uniform Temperature. Obviously if the Body is to preserve the same temperature during any period of time the production of heat within it must exactly balance the loss of heat from it during that time. In ourselves this balance is actually maintained within narrow limits of fluctuation throughout healthy life. Only in fevers, or as the result of prolonged exposure to cold, is the balance upset. In fact its preservation is necessary for the continuance of the life of a warm-blooded animal; should the temperature rise above certain limits chemical changes, incompatible with life, occur in the tissues; for example, at about 45° C. (113° F.) the muscles begin to become rigid. On the other hand, death ensues if the Body be cooled down to about 19° C. (66° F.).

Since we live in an environment of constantly varying temperature a rather delicate adjustment between heat-production and heat-loss is required.

This adjustment is attained through the interaction of two sorts of regulatory devices, one for controlling the loss of heat from the Body, the other its production in the Body. Both of these are partly voluntary and partly involuntary. As regards heat-loss, by far the most important regulating organ is the skin: under ordinary circumstances nearly 90 per cent of the total heat given off from the Body in 24 hours goes by the skin (73 by radia-

tion and conduction, 14.5 by evaporation of sweat). This loss may be controlled:

1. By *clothing;* we naturally wear more in cold and less in warm weather; the effect of clothes being, of course, not to warm the Body but to diminish the rate at which the heat produced in it is lost.

2. *Automatically*, through the operation of the *temperature-regulating mechanism.* This mechanism consists of a "temperature center" in the medulla, together with afferent nerves to it from the temperature receptors in the skin; efferent nerves from it to the blood vessels and sweat-glands at the surface of the Body; and these vessels and glands as end organs through which the actual regulation is effected.

The temperature center is susceptible to influences coming to it from the temperature receptors in the skin, and also to changes in the temperature of the blood flowing directly through it. The center is stimulated to discharge by impulses from the warmth receptors, and also by a rise in the temperature of the blood. Whenever discharges take place the blood vessels of the skin become dilated (and the skin correspondingly red) and the sweat-glands pour out sweat freely. When there is a lowering of the temperature of the blood, or impulses from the receptors for cold, the activity of the center is diminished or suppressed; the skin-vessels become constricted (and the skin pale) and the sweat-glands cease to function, or function so slightly that sweat is not in evidence.

It is obvious that these two agencies, cutaneous circulation and sweat secretion, operate together to favor or hamper loss of heat. Under the influence of the temperature center their action is thus jointly directed to the same end. A very interesting fact of nerve Physiology is that while the efferent nerves to the sweat-glands are part of the thoracico-lumbar system, those to the vasodilators of the skin belong rather to the cranial subdivision of the autonomic system, the thoracico-lumbar innervation to the vessels being constrictor. The consequence of this is that any condition which is attended by a general outpouring over the thoracico-lumbar system, fright for example (p. 209), causes sweat to be secreted upon a skin in which vasoconstriction is occurring, and which is therefore cool. This is the explanation of the "cold sweat" of terror.

Of comparatively little importance in man, but of great importance in fur-bearing animals, is the loss of heat through the lungs. In warm weather there is quickened respiration, brought about reflexly through the play of cutaneous sensory impulses of warmth upon the respiratory center. This quickened respiration carries off heat more rapidly both by increasing the amount of air warmed to body temperature in a given time, and by increasing the evaporation of water from the lungs.

Fever. Strictly speaking any sustained body-temperature higher than normal by as much as a degree constitutes fever. Whenever heat-loss falls behind heat-production, no matter how caused, the temperature must rise and keep on rising until equality is re-established on a higher temperature level, known as the fever temperature. Ordinary fevers are due to a disturbance of the temperature center of such a sort that higher blood-temperatures than normal are necessary to cause it to discharge. The center is also less sensitive than usual to afferent impulses from the warmth receptors. These changes in sensitivity are attributed, in ordinary infectious fevers, to poisoning by the toxins of the disease (p. 322); fever is therefore a secondary factor in infection, rather than a primary. As the temperature rises the bodily oxidations become more rapid, since they are like other chemical processes in being hastened by rise in temperature. The increased heat-production thus brought about is not, however, the major factor in fever, since it is much less than attends almost any vigorous muscular exercise. After the fever temperature is established heat-loss again keeps pace with heat-production, but, as is well known, more by very pronounced vasodilation than by stimulation of sweat-secretion. Thus we have the characteristic flushed dry skin of fever.

Factors Influencing Heat-Production. As regards temperature regulation by modifying the rate of heat-production in the Body, the following points may be noted: on the whole such regulation is far less important than that brought about by changes in the rate of loss, since the necessary vital work of the Body always necessitates the continuance of oxidative processes which liberate a tolerably large quantity of heat. The Body cannot therefore be cooled by diminishing such oxidations beyond a certain limit; nor, on the other hand, can it be warmed indefinitely by increasing

them. Still, within certain limits, the heat-production may be controlled in several ways:

1. In cold weather there is an increased appetite for protein foods. The increased consumption of proteins leads, through their *specific dynamic action* (p. 541) to greater oxidative activity, and so to increased heat-production.

2. Under the stimulus of cold the adrenal glands are stimulated to increased production of adrenin; this substance, as stated formerly (p. 26), is a hydrogen transporter, and therefore augments bodily oxidations in proportion to the amount of it present (p. 528). When the adrenal glands are excited to activity under the influence of cold, therefore, the resulting outpouring of adrenin causes an increased oxidation of fuel, with corresponding production of additional heat.

3. When the cooling persists beyond the ability of increased adrenin output to counteract it, reflex activity of skeletal muscles is set in play. This takes the form first of increased skeletal muscle tonus (p. 135), which we appreciate in ourselves as "resisting the cold." Then reflex shivering and chattering of the teeth come on. These latter actions involve many muscle-fibers and so give rise to considerable heat; they represent the utmost the Body does in the way of automatic increase in heat production. If they fail to maintain the body-temperature at its normal level either a fall in temperature will occur or voluntary means of preventing it must be resorted to.

4. Voluntary muscular exercise is the obvious resort when shivering fails to overcome chilliness. By vigorous exercise large heat-production can be induced; sufficient, indeed, to enable one to keep warm in very severe weather. Conversely, one inclines to be idle in warm weather; by keeping heat-production at the minimum the heat-loss mechanism is more readily able to eliminate heat as fast as produced, even in spite of the handicap presented by a warm environment.

We have to recognize that in man, with his naked skin, these mechanisms are not sufficient to enable him, without other aid, to inhabit regions in which severe cold occurs at times. Only because he has sufficient intelligence to plan for and use such artificial devices as clothing, shelter, and fire, is it possible for him to live outside the tropics.

Clothing. While the majority of other warm-blooded animals have coats of their own, formed of hairs or feathers, over most of man's Body his hairy coating is merely rudimentary and has lost nearly all physiological importance as a protection from cold; except in tropical regions he has to protect himself by artificial garments, which his esthetic sense has led him to utilize also for purposes of adornment. Here, however, we must confine ourselves to clothes from a physiological point of view. In civilized societies every one is required to cover most of his Body with something, and the question is what is the best covering; the answer will vary, of course, with the climatic conditions of the country dwelt in. In warm countries, clothing, in general terms, should allow free radiation or conduction of heat from the surface; in cold it should do the reverse; and in temperate climates, with varying temperatures, it should vary with the season. If the surface of the Body be exposed so that currents of air can freely traverse it much more heat will be carried off (under those usual conditions in which the air is cooler than the skin) than if a stationary layer of air be maintained in contact with the surface. As every one knows, a "draught" cools much faster than air of the same temperature not in motion. All clothing, therefore, tends to keep up the temperature of the Body by checking the renewal of the layer of air in contact with it. Apart from this, however, clothes fall into two great groups: those which are good, and those which are bad, conductors of heat. The former allow changes in the external temperature to cool or heat rapidly the air stratum in actual contact with the Body, while the latter only permit these changes to act more slowly. Of the materials used for clothes, linen is the best conductor, and therefore makes the coolest garments; cotton and silk conduct somewhat less well; wool and fur are bad conductors, and therefore make the warmest garments.

Common Colds. The infections with which we are most frequently beset are grouped under the designation of *common colds;* although apparently due to a number of different organisms the symptoms are similar, and the conditions enabling the organisms to obtain a foothold are also very much the same. It appears that the organisms are so prevalent that we can scarcely draw a breath without inhaling some of them; indeed they are probably present nearly all the time on the mucous linings of the respiratory

tract. So long as the cells of these linings are in prime condition, and adequately nourished by an abundant blood-flow through the vessels underlying them, they present an effective barrier to the entry of the organisms into the Body (p. 322). Should pronounced vasoconstriction occur in these vessels, cutting down the blood-flow materially, the membranes are apt to suffer undernourishment for the time being, and while so suffering may become passable to the "cold" organisms. It has been shown recently that sudden chilling of the skin causes constriction of the vessels in the mucous membranes, along with constriction in the skin vessels themselves. Thus we see in sudden chilling a starting point for conditions likely to lead to "taking cold." The obvious precaution is to avoid sudden chilling, as by sitting in a draught, especially when breathing air in which the organisms are likely to be present. Other conditions leading to vasoconstriction of skin and mucous membranes are to be avoided as well. Sitting still with wet feet is a good example of a condition of this sort. Simple colds may cause, of themselves, nothing worse than a loss of efficiency for a few days, but they may open the way to infection with much more dangerous organisms, particularly of tuberculosis, pneumonia, and influenza. Hence one is well advised to guard as effectively as possible against taking cold.

CHAPTER XXXIII

VOICE AND SPEECH

Voice consists of sounds produced by the vibrations of two elastic bands, the *true vocal cords*, placed in the *larynx*, an upper modified portion of the passage which leads from the pharynx to the lungs. When the vocal cords are put in a certain position, air driven past them sets them in vibration, and they emit a musical note; the lungs and respiratory muscles are, therefore, accessory parts of the vocal apparatus: the strength of the blast produced by them determines the *loudness* of the voice. The larynx itself is the essential voice-organ: its size primarily determines the *pitch* of the voice, which is lower the longer the vocal cords; and, hence, shrill in children, and usually higher pitched in women than in men; the male larynx grows rapidly at commencing manhood, causing the change commonly known as the "breaking of the voice." Every voice, while its general pitch is dependent on the length of the vocal cords, has, however, a certain range, within limits which determine whether it shall be soprano, mezzo-soprano, alto, tenor, baritone, or bass. This variety is produced by muscles within the larynx which alter the tension of the vocal cords. Those characters of voice which we express by such phrases as harsh, sweet, or sympathetic, depend on the structure of the vocal cords of the individual; cords which in vibrating emit only harmonic overtones (Chap. XIV) are pleasant; while those in which inharmonic overtones are conspicuous are disagreeable.

The vocal cords alone would produce but feeble sounds; those that they emit are strengthened by sympathetic resonance of the air in the pharynx and mouth, the action of which may be compared to that of the sounding-board of a violin. By movements of throat, soft palate, tongue, cheeks, and lips the sounds emitted from the larynx are altered or supplemented in various ways, and converted into articulate language or *speech*.

The Larynx lies in front of the neck, beneath the hyoid bone and above the windpipe; in many persons it is prominent, causing the projection known as "Adam's apple." It consists of a

framework of cartilages, partly joined by true synovial joints and partly bound together by membranes; muscles are added which move the cartilages with reference to one another; and the whole is lined by a mucous membrane.

The cartilages of the larynx (Fig. 150) are nine in number; three single and median, and three pairs. The largest (*t*) is called the *thyroid*, and consists of two halves which meet at an angle in front, but separate behind so as to inclose a V-shaped space, in which most of the remaining cartilages lie. The *epiglottis* (not represented in the figure) is fixed to the top of the thyroid cartilage and overhangs the entry from the pharynx to the larynx; it may be seen, covered by mucous membrane, projecting at the base of the tongue, if the latter be pushed down while the mouth is held open in front of a mirror; and is, similarly covered, represented, as seen from behind, at *a* in Fig. 151. The *cricoid*, the last of the unpaired cartilages, has the shape of a signet-ring; its broad part (**, Fig. 150) is on the posterior side and lies at the lower part of the opening between the halves of the thyroid; in front and on the sides it is narrow, and a space, occupied by the *crico-thyroid membrane*, intervenes between its upper border and the lower edge of the thyroid cartilage. The angles of the latter are produced above and below into projecting *horns* (*Cs* and *Ci*, Fig. 150), and the lower horn on each side forms a joint with the cricoid. The thyroid can be rotated on an axis, passing through the joints on each side, and rolled down so that its lower front edge shall come nearer the cricoid cartilage, the membrane there intervening being folded. The *arytenoids* (†, Fig. 150) are the largest of the paired cartilages; they are seated on the upper edge of the posterior

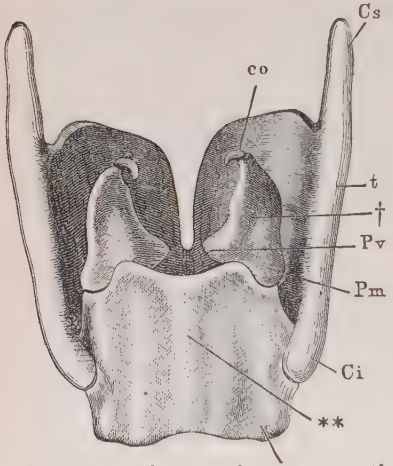


FIG. 150.—The more important cartilages of the larynx from behind. *t*, thyroid; *Cs*, its superior, and *Ci*, its inferior, horn of the right side; **, cricoid cartilage; †, arytenoid cartilage; *Pv*, the corner to which the posterior end of a vocal cord is attached; *Pm*, corner on which the muscles which approximate or separate the vocal cords are inserted; *co*, cartilage of Santorini.

wide portion of the cricoid, and form true joints with it. Each is pyramidal with a triangular base, and has on its tip a small nodule (*co*, Fig. 150), the *cartilage of Santorini*. From the tip of each arytenoid cartilage *the aryteno-epiglottic fold* of mucous membrane (10, Fig. 151) extends to the epiglottis; the cartilage of Santorini causes a projection (8, Fig. 151) in this, and a little farther on (9) is a similar eminence on each side, caused by the remaining pair of cartilages, known as the *cuneiform*, or cartilages of *Wrisberg*.

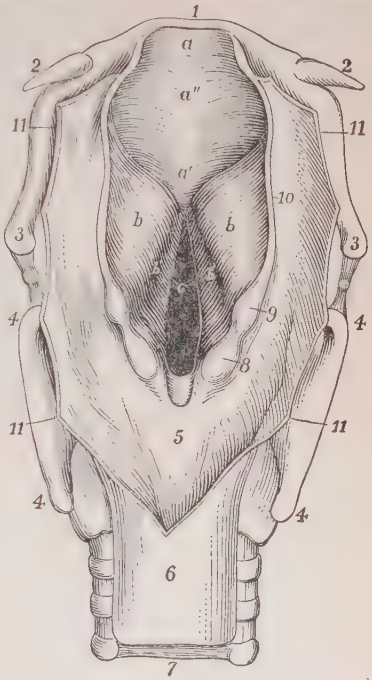


Fig. 151.—The larynx viewed from its pharyngeal opening. The back wall of the pharynx has been divided and its edges (11) turned aside. 1, body of hyoid; 2, its small, and 3, its great, horns; 4, upper and lower horns of thyroid cartilage; 5, mucous membrane of front of pharynx, covering the back of the cricoid cartilage; 6, upper end of gullet; 7, windpipe, lying in front of the gullet; 8, eminence caused by cartilage of Santorini; 9, eminence caused by cartilage of Wrisberg; both lie in, 10, the *aryteno-epiglottic fold* of mucous membrane, surrounding the opening (*aditus laryngis*) from pharynx to larynx. *a*, projecting tip of epiglottis; *c*, the glottis, the lines leading from the latter point to the free vibratory edges of the vocal cords. *b'*, the ventricles of the larynx; their upper edges, marking them off from the eminences *b*, are the false vocal cords.

The Vocal Cords are bands of elastic tissue which reach from the inner angle (*Pv*, Fig. 150) of the base of each arytenoid cartilage to the angle on the inside of the thyroid where the sides of the *V* unite; they thus meet in front but are separated at their other ends. The cords are not, however, bare strings, like those of a harp, but covered over with the lining mucous membrane of the larynx, a slit, called the *glottis* (*c*, Fig. 151), being left between them. It is the projecting cushions formed by them on each side of this slit which are set in vibration during phonation. Above each vocal cord is a depression, the *ventricle of the larynx* (*b'*, Fig. 151); this is bounded above by a somewhat prominent edge, *the false vocal cord*. Over most of the interior of the larynx its mucous membrane is thick and covered by ciliated

epithelium, and has many mucous glands imbedded in it. Over the vocal cords, however, it is represented only by a thin layer of flat nonciliated cells, and contains no glands. In quiet breathing, and after death, the free inner edges of the vocal cords are thick and rounded, and seem very unsuitable for being readily set in vibration. They are also tolerably widely separated behind, the arytenoid cartilages, to which their posterior ends are attached, being separated. Air under these conditions passes through without producing voice. If they are watched with the laryngoscope during phonation, it is seen that the cords approximate behind so as to narrow the glottis; at the same time they become more tense, and their inner edges project more sharply and form a better-defined margin to the glottis, and their vibrations can be seen. These changes are brought about by the delicately co-ordinated activity of a number of small muscles, which move the cartilages to which the cords are fixed.

The Muscles of the Larynx. In describing the direction and action of these it is convenient to use the words front or anterior and back or posterior with reference to the larynx itself (that is, as equivalent to ventral and dorsal) and not with reference to the head, as usual. The base of each arytenoid cartilage is triangular and fits on a surface of the cricoid, on which it can slip to and fro to some extent, the ligaments of the joint being lax. One corner of the triangular base is directed inwards and forwards (*i. e.*, towards the thyroid) and is called the *vocal process* (*Pv*, Fig. 150), as to it the vocal cords are fixed. The outer posterior angle (*Pm*, Fig. 150) has several muscles inserted on it and is called the *muscular process*. If it be pulled back and towards the middle line the arytenoid cartilage will rotate on its vertical axis, and roll its vocal processes forwards and outwards, and so widen the glottis; the reverse will happen if the muscular process be drawn forwards. The muscle producing the former movement is the *posterior crico-arytenoid* (*Cap*, Fig. 152); it arises from the back of the cricoid cartilage, and narrows to its insertion into the muscular process of the arytenoid on the same side. The opponent of this muscle is the *lateral crico-arytenoid*, which arises from the side of the cricoid cartilage, on its inner surface, and passes upwards and backwards to the muscular process. The posterior crico-arytenoids, working alone, pull inwards and downwards the muscular processes, turn

upwards and outwards the vocal processes, and separate the posterior ends of the vocal cords. The lateral cricothyroid, working alone, pulls downwards and forwards the muscular process, and rotates inwards and upwards the vocal process, and narrows the glottis; it is the chief agent in producing the approximation of the cords necessary for the production of voice. When both pairs of muscles act together, however, each neutralizes the tend-

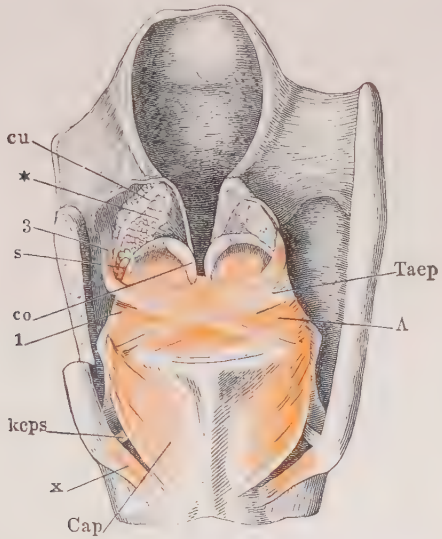


FIG. 152.—The larynx seen from behind and dissected so as to display some of its muscles. The mucous membrane of the front of the pharynx (5, Fig. 150) has been dissected away, so as to display the laryngeal muscles beneath it. Part of the left half of the thyroid cartilage has been cut away. *co*, cartilage of Santorini; *cu*, cartilage of Wrisberg.

ency of the other to rotate the arytenoid cartilage; the downward part of the pull of each is, thus, alone left, and this causes the arytenoid to slip downwards and outwards, off the eminence on the cricoid with which it articulates, as far as the loose capsular ligament of the joint will allow. The arytenoid cartilages are thus moved apart and the glottis greatly widened and brought into its state in deep quiet breathing. Other muscles approximate the arytenoid cartilages after the cartilages have been separated. The most important is the *transverse arytenoid* (*A*, Fig. 152), which runs across from one arytenoid cartilage to the other.

Another is the *oblique arytenoid* (*Taep*), which runs across the middle line from the base of one arytenoid to the tip of the other; thence certain fibers continue in the aryteno-epiglottic fold (10, Fig. 151) to the base of the epiglottis; this, with its fellow, embraces the whole entry to the larynx; when they contract they bend inwards the tips of the arytenoid cartilages, approximate the edges of the aryteno-epiglottic fold, and draw down the epiglottis, and so close the passage from the pharynx to the larynx. When the epiglottis has been removed, food and drink rarely enter the larynx in swallowing, the folds of mucous membrane being so brought together as to close the aperture between them effectually.

Increased tension of the vocal cords is produced by the *crico-thyroid muscles*, one of which lies on each side of the larynx, over the cricothyroid membrane. Their action may be understood by help of the diagram, Fig. 153, in which *t* represents the thyroid cartilage, *c* the cricoid, *a* an arytenoid, and *vc* a vocal cord. The muscle passes obliquely backwards and upwards from about *d* near the front end of *c*, to about *l*, on the thyroid cartilage *t*, near the pivot (which represents the joint between the cricoid cartilage and the inferior horn of the thyroid). When the muscle contracts it pulls together the anterior ends of *t* and *c;* either by depressing the thyroid (as represented by the dotted lines) or by raising the front end of the cricoid; and thus stretches the vocal cord, if the arytenoid cartilages be held from slipping forwards. The antagonist of the cricothyroid is the *thyro-arytenoid muscle;* it lies, on each side, imbedded in the fold of elastic tissue forming the vocal cord, and passes from the inside of the angle of the thyroid cartilage in front, to the anterior angle and front surface of the arytenoid behind. If the latter be held firm, the muscle raises the thyroid cartilage from the position into which the cricothyroid pulls it down, and so slackens the vocal cords. If the thyroid be held fixed by the cricothyroid muscle, the thyro-arytenoid will help to approximate the vocal cords, rotating inwards the vocal processes of the arytenoids.

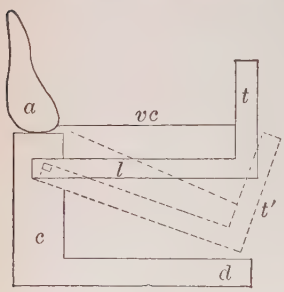


FIG. 153.

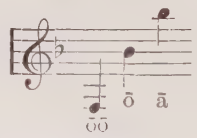
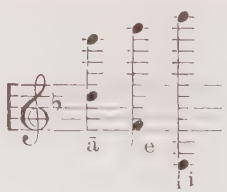
The lengthening of the vocal cords when the thyroid cartilage

is depressed tends to lower their pitch; the increased tension, however, more than compensates for this and raises it. There seems, however, still another method by which high notes are produced. Beginning at the bottom of his register, a singer can go up the scale some distance without a break; but, then, to reach his higher notes, must pause, rearrange his larynx, and begin again. What happens is that, at first, the vocal processes are turned in, so as to approximate but not to meet; the whole length of each edge of the glottis then vibrates, and its tension is increased, and the pitch of the note raised, by increasing contraction of the cricothyroid. At last this attains its limit and a new method has to be adopted. The vocal processes are more rolled in, until they touch. This produces a node (see Physics) at that point and shortens the length of vocal cord which vibrates. The shorter string emits a higher note; so the cricothyroid is relaxed, and then again gradually tightened as the notes sung are raised in pitch from the new starting-point. To pass easily and imperceptibly from one such arrangement of the larynx to another is a great art in singing. There is some reason to believe that a second node may, for still higher notes, be produced at a more anterior point on the vocal cords.

The method of production of *falsetto notes* is uncertain; during their emission the free border of the vocal cords alone vibrates.

The range of the human voice is about three octaves, from *e* (80 vib. per 1″) on the unaccented octave, in male voices, to *c* on the thrice-accented octave (1,024 vib. per 1″), in female. Great singers of course go beyond this range; basses have been known to take *a* on the great octave (55 vib. per 1″); and Nilsson in "Il Flauto Magico" used to take *f* on the fourth accented octave (1,408 vib. per 1″). Mozart heard at Parma, in 1770, an Italian songstress whose voice had the extraordinary range from *g* in the first accented octave (198 vib. per 1″) to *c* on the fifth accented octave (2,112 vib. per 1″). An ordinary good bass voice has a compass from *f* (88 vib. per 1″) to *d″* (297 vib. per 1″); and a soprano from *b′* (248 vib. per 1″) to *g‴* (792).

Vowels are, primarily, compound musical tones produced in the larynx. Accompanying the primary tone of each, which determines its pitch when said or sung, are a number of overtones, the first five or six being recognizable in good full voices. Certain of these overtones are reinforced in the mouth to produce one

vowel, and others for other vowels; so that the various vowel sounds are really musical notes differing from one another in quality or timbre. The mouth and throat cavities form an air-chamber above the larynx, and this has a note of its own which varies with its size and form, as may be observed by opening the mouth widely, with the lips retracted and the cheeks tense; then gradually closing it and protruding the lips, meanwhile tapping the cheek. As to the mouth changes its form the note produced changes, tending in general to pass from a higher to a lower pitch and suggesting to the ear at the same time a change from the sound of å (*f*a*ther*) through ō (m*o*re) to o͞o (m*oo*r). When the mouth and throat chambers are so arranged that the air in them has a vibratory rate in unison with any overtone in the laryngeal tone, it will be set in sympathetic vibration, that overtone will be strengthened, and the vowel characterized by it uttered. As the mouth alters its form, although the same note be still sung, the vowel changes. In the above series (å, ō, o͞o) the tongue is depressed and the cavity forms one chamber; for å this has a wide mouth opening; for ō it is narrowed; for o͞o still more narrowed, and the lips protruded so as to increase the length of the resonance chamber. The overtones reinforced in each case are, according to Helmholtz—

In other cases the mouth and throat cavity is partially subdivided by elevating the tongue, into a wide posterior and a narrow anterior part, each of which has its own note; and the vowels thus produced owe their character to two reinforced overtones. This is the case with the series ă (m*a*n), e (th*e*re), and i (mach*i*ne), the tones reinforced by resonance in the mouth being—

The usual ī of English, as in spire, is not a true simple vowel but a diphthong, consisting of ă (pad) followed by ē (feet), as may be observed by trying to sing a sustained note to the sound ī; it will then be seen that it begins as ă and ends as ēe. A simple vowel can be maintained pure as long as the breath holds out.

In uttering true vowel sounds the soft palate is raised so as to cut off the air in the nose, which, thus, does not take part in the sympathetic resonance. For some other sounds (the *semi-vowels* or *resonants*) the initial step is, as in the case of the true vowels, the production of a laryngeal tone; but the soft palate is not raised, and the mouth exit is more or less closed by the lips or the tongue; hence the blast partly issues through the nose, and the air there takes part in the vibrations and gives them a special character; this is the case with *m*, *n*, and *ng*.

Consonants are sounds produced not mainly by the vocal cords, but by modifications of the expiratory blast on its way through the mouth. The current may be interrupted and the sound changed by the lips (*labials*); or, at or near the teeth, by the tip of the tongue (*dentals*); or, in the throat, by the root of the tongue and the soft palate (*gutturals*). Consonants are also characterized by the kind of movement which gives rise to them. In *explosives* an interruption to the passage of the air-current is suddenly interposed or removed (P, T, B, D, K, G). Other consonants are *continuous* (as F, S, R), and may be subdivided into: (1) *Aspirates*, characterized by the sound produced by a rush of air through a narrow passage, as when the lips are approximated (F), or the teeth (S), or the tongue is brought near the palate (Sh), or its tip against the two rows of teeth, they not being quite in contact (Th). For L the tongue is put against the hard palate and the air escapes on its sides. For Ch (as in the proper Scotch pronunciation of *loch*) the passage between the back of the tongue and the soft palate is narrowed. To many of the above pure consonants answer others, in whose production true vocalization (*i. e.*, a laryngeal tone) takes a part. F with some voice becomes V; S becomes Z, Th soft (teeth) becomes Th hard; and Ch becomes Gh. (2) *Resonants;* these have been referred to above. (3) *Vibratories* (the different forms of R), which are due to vibrations of

parts bounding a constriction put in the course of the air-current. Ordinary R is due to vibrations of the tip of the tongue held near the hard palate; and guttural R to vibrations of the uvula and parts of the pharynx.

The consonants may physiologically be classified as in the following table (Foster):

Explosives.	*Labials*, without voice	P.
	" with voice	B.
	Dentals, without voice	T.
	" with voice	D.
	Gutturals, without voice	K.
	" with voice	G (hard).
Aspirates.	*Labials*, without voice	F.
	" with voice	V.
	Dentals, without voice	S, L, Sh, Th (hard).
	" with voice	Z, Zh (azure), Th (soft).
	Gutturals, without voice	Ch (loch).
	" with voice	Ch.
Resonants.	*Labial*	M.
	Dental	N.
	Gutteral	NG.
Vibratories.	*Labial*—not used in European languages.	
	Dental	R (common).
	Guttural	R (guttural).

H is a laryngeal sound: the vocal cords are separated for its production, yet not so far as in quiet breathing. The air-current then produces a friction sound but not a true note, as it passes the glottis; and this is again modified when the current strikes the wall of the pharynx. Simple sudden closure of the glottis, attended with no sound, is also a speech element, though we do not indicate it with a special letter, since it is always understood when a word begins with a vowel, and only rarely is used at other times. The Greeks had a special sign for it, ', the *soft breathing;* and another, ', the *hard breathing*, answering somewhat to our *h* and indicating that the larynx was to be held open, so as to give a friction sound, but not voice.

In whispering there is no true voice; the latter implies true *tones*, and these are only produced by periodic vibrations; whispering is a *noise*. To produce it the glottis is considerably narrowed but the cords are not so stretched as to produce a sharply defined

edge on them, and the air driven past is then thrown into irregular vibrations. Such vibrations as coincide in period with the air in the mouth and throat are always present in sufficient number to characterize the vowels; and the consonants are produced in the ordinary way, though the distinction between such letters as P and B, F and V, remains imperfect.

CHAPTER XXXIV

REPRODUCTION

Reproduction in General. In all cases reproduction consists, essentially, in the separation of a portion of living matter from a parent; the separated part bearing with it, or *inheriting*, certain tendencies to repeat, with more or less variation, the life history of its progenitor. All living things, both plant and animal, are so complex (bacteria perhaps excepted; we know little about the details of reproduction in them) that the separation off of a piece which shall repeat the main features of the parent involves an elaborate mechanism. In reproduction in the higher forms two parents contribute jointly to the protoplasmic beginning-cell (fertilized ovum) which develops into the offspring. This joint contribution complicates the mechanism still more. To introduce the account we shall deal first, therefore, with the simpler process of cell-division as it occurs during growth in all multicellular organisms, and in some tissues throughout life in adult man (p. 32).

Cell-Division. In the formation of a particular kind of tissue, or in the perpetuation of such kinds as continue to multiply throughout life, the daughter-cells are ordinarily precisely like the mother-cell whose division brings them into existence. This likeness is insured by a device which partitions the determiners of hereditary traits (present in the mother-cell nucleus) exactly between the daughter-cell nuclei. These determiners, known as *genes*, are located in nuclear structures called *chromosomes*. In a resting cell the chromosomes are so intermingled and distorted in outline that their identity is impossible to make out; what is seen is a fine network, or sponge-like mass, of substance that takes stains particularly well, and hence is known as *chromatin*. The only special chemical characteristic of it, at present known, is that it contains a high percentage of nucleo-proteins (Chap. I).

The first thing that happens in an incipient dividing cell is the arrangement of the chromatin material into a single strand, more or less twisted about, and called the *spireme* (*s*, Fig. 154, 1). About

the same time the cytoplasm begins to show minute fibers projecting from points on opposite sides of the nucleus toward various places on the spireme. These fibers are known as *spindle fibers* (since all together they form a sort of spindle), and the points

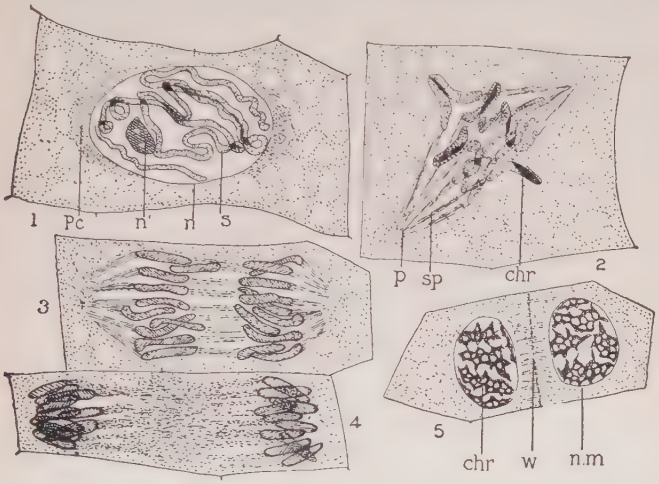


Fig. 154.—Selected Stages in Cell Division of Cells of the Root Tip of the Spiderwort. 1. The chromatin has organized itself into a long slender thread or spireme and the cytoplasm begins to show indications of the organization of the spindle. 2. The spireme has broken into fragments, the chromosomes, each of which is split lengthwise and arranged at the middle of the spindle where the two exactly equivalent halves are being separated. 3. The halves are completely separate and moving toward their respective poles of the spindle. 4. The chromosomes have arrived at the poles and are aggregated in a close mass but have not yet been surrounded by a nuclear membrane. 5. The nuclear membrane and nuclear sap have formed and the chromosomes are beginning to undergo a process of vacuolation which will eventually reduce each one to a state more or less resembling a very much broken rubber sponge. *p.c.*, polar cap of cytoplasm out of which the spindle fibers are organized; *n.m.*, nuclear membrane; *s*, spireme; *n'*, nucleolus; *sp*, spindle fibers; *p*, pole of spindle; *chr*, chromosomes.

from which they diverge are the poles of the spindle (*sp* and *p*, Fig. 154, 2).

The next stage is one in which the spireme breaks up into a definite number of pairs of structures, called *chromosomes*, constant for all the cells of each species (except at one stage in reproduction as described below), but varying in number from a single pair in some forms to at least sixty-four in others. In man twenty-four pairs are present. The form selected for illustration in the figure has five pairs, or ten chromosomes in all. Following the breaking of the spireme into individual chromosomes spindle fibers from

both poles become attached to opposite sides of each chromosome, and each then begins to split lengthwise into exactly equal halves (Fig. 154, 2). The halves separate and travel (or are drawn) toward opposite poles as shown in 3 and 4 of the figure. After reaching the poles they merge into chromatin networks similar to that seen in the resting mother-cell, and the cytoplasm divides, giving two daughter-cells, each just like the mother-cell except smaller (Fig. 154, 5). The lengthwise splitting of the chromosomes is considered to split each gene or hereditary determiner into equal parts, of which each daughter-cell receives one. The whole mechanism of cell-division (known as *mitosis*) is directed toward this end.

Germ-Cells Compared with Tissue-Cells. Those cells which are set apart for the maintenance of the race are called *germ*-cells to distinguish them from the cells which make up the Body generally and which are designated as *somatic* cells. Each individual is derived from a single germ-cell, as noted in an earlier chapter (p. 37), by a process of cell multiplication and cell differentiation. The germinal tissues are tissues in which germ-cells occur as the main cells, but which contain also various supporting cells, and have numerous blood vessels penetrating them. The characteristic activity of germinal tissues is multiplication of germ-cells, as described in detail below (p. 595). The germ-cells themselves are undifferentiated, as indeed they must be, since from them are derived all the kinds of highly differentiated cells found in the fully developed Body.

Sexual Reproduction. In some cases, especially among insects, the reproductive cells of the female can develop, under suitable conditions, wholly of and by themselves, and give rise to new individuals; such a mode of reproduction is called *parthenogenesis:* but in the majority of cases, and always in the higher animals, this is not so; the fusion of two cells is a necessary preliminary to development. Commonly the coalescing cells differ considerably in size and form, and one takes a more direct share in the developmental processes; this is the egg-cell or *ovum;* the other is the *sperm-cell* or spermatozoön. The fusion of the two is known as *fertilization.* Animals producing both ova and spermatozoa are *hermaphrodite;* those bearing ova only, *female;* and those spermatozoa only, *male:* hermaphroditism is not found in Vertebrates, except in rare and doubtful cases of monstrosity.

Maturation of the Germ-Cells. In the germinal tissues of the sexually mature individual cell multiplication goes on actively by the process of mitosis described above. At a certain stage, however, every germ-cell passes through a modified mitosis to fit it for taking part in the reproductive cycle. An essential feature of reproduction in higher forms, as noted in the last paragraph, is fertilization, or the fusion of two germ-cells, male and female. This fusion, by adding the chromosomes of the male cell to those of the female, would double the number in the fertilized egg were not some arrangement provided to avoid it. This arrangement is found in the modified mitosis just mentioned, to which is given the name *maturation* or ripening of the germ-cell. We will recall from the earlier description of mitosis that the chromatin forms itself into a definite number of chromosomes, and that each chromosome splits *lengthwise* in such fashion that half of it goes to each daughter-cell. Thus the daughter-cells are exactly alike so far as chromosome content goes. In the process of maturation the chromosomes do not split lengthwise. Instead *half of them* pass to one daughter-cell and *half* to the other. Thus we have a reduction of the number of chromosomes to half the original. Moreover, since no two chromosomes are apt to be alike, even though belonging to the same pair (see below), the daughter-cells of this division differ in chromosome content, a fact that is highly significant in heredity, since the chromosomes carry the determiners of hereditary traits.

In the formation of *sperm* the daughter-cells of the maturation or *reduction* division (so called because it reduces the number of chromosomes), are of equal size and equal importance. Each undergoes an additional mitosis of the ordinary type, so that from each primary sperm-forming cell four functional spermatozoa are derived. The *ovum* furnishes the main mass of cytoplasm from which development is to proceed. Its maturation takes place in such a fashion that the cell mass as a whole is undisturbed by the changes taking place in the chromatin. The *reduction division* occurs with the chromosomes of the ovum, precisely as in the primary sperm-cell; but instead of this chromosome division being followed by ordinary cell division, the division is unequal. Most of the cell substance continues as before, retaining half the chromosomes. A very small amount is set apart with the other half of the chromosomes, and serves no useful purpose. This is

known as the *first polar body*. At this stage the ovum and the polar body are comparable to the daughter-cells of the reduction division of the primary sperm-forming cell. There is an additional mitosis in ovum and polar body just as in the sperm formers. The polar body divides into two of equal size. The division of the ovum is again unequal, and an additional polar body is formed. At the end of maturation of the egg, therefore, we have four cells corresponding to the four sperms, but one of them has retained virtually all the cell substance, and is the functional ovum. Figure 155 is a diagram illustrating the stages of maturation. The ovum

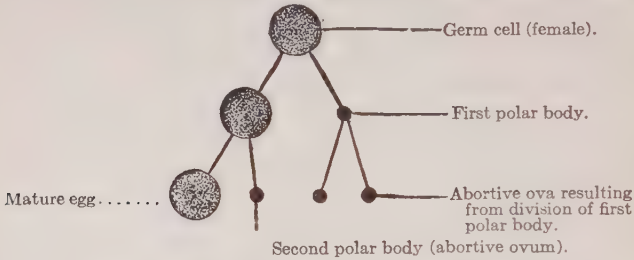

Germ cell (female).
First polar body.
Mature egg.....
Abortive ova resulting from division of first polar body.
Second polar body (abortive ovum).

FIG. 155.—Diagram showing the genesis of the egg (after Boveri). A similar diagram in which all the daughter cells were of equal size would serve to illustrate the genesis of spermatozoa.

and the sperm each contain half the original number of chromosomes. When they fuse in the process of fertilization the full number is restored.

Accessory Reproductive Organs. The organ in which ova are produced is known as the *ovary*, that forming spermatozoa, as the *testis* or *testicle;* but in different groups of animals many additional accessory parts may be developed. Thus, in all but the very lowest Mammalia, the offspring is nourished for a considerable portion of its early life within the body of its mother, a special cavity, the *uterus* or *womb*, being provided for this purpose: the womb communicates with the exterior by a passage, the *vagina;* and two tubes, the *oviducts* or *Fallopian tubes*, convey the eggs to it from the *ovaries*. In addition, *mammary glands* provide milk for the nourishment of the young in the first months after birth. In the male mammal we find as accessory reproductive organs, *vasa deferentia* which convey from the testes the seminal fluid containing spermatozoa; *vesiculæ seminales* (not present in all Mammalia), glands whose secretion is mixed with that of the

testes or is expelled after it in the sexual act; a *prostate gland*, whose secretion is added to the semen; and an erectile organ, the *penis*, by which the fertilizing liquid is conveyed into the vagina of the female.

The Male Reproductive Organs. The testes in man are paired tubular glands, which lie in a pouch of skin called the *scrotum*. This pouch is subdivided internally by a partition into right and left chambers, in each of which a testicle lies. The chambers are lined inside by a serous membrane, the *tunica vaginalis*, and this doubles back (like the pleura round the lung) and covers the exterior of the gland. Between the external and reflected layers of the tunica vaginalis is a space containing a small quantity of lymph.

The testicles develop in the abdominal cavity, and only later (though commonly before birth) descend into the scrotum, passing through apertures in the muscles, etc., of the abdominal wall, and then sliding down over the front of the pubes, beneath the skin. The cavity of the tunica vaginalis at first is a mere offshoot of the peritoneal cavity, and its serous membrane is originally a part of the peritoneum. In the early years of life the passage along which the testis passes usually becomes nearly closed up, and the communication between the peritoneal cavity and that of the tunica vaginalis is also obliterated. Traces of this passage can, however, readily be observed in male infants; if the skin inside the thigh be tickled a muscle lying beneath the skin of the scrotum is made to contract reflexly, and the testis is jerked up some way towards the abdomen and quite out of the scrotum. Sometimes the passage remains permanently open and a coil of intestine may descend along it and enter the scrotum, constituting an *inguinal hernia or rupture*. A *hydrocele* is an excessive accumulation of liquid in the serous cavity of the tunica vaginalis.

Beneath its covering of serous membrane each testis has a proper fibrous tunic of its own. This forms a thick mass on the posterior side of the gland, from which partitions or *septa* (*i*, Fig. 156) radiate, subdividing the organ into many chambers. In each chamber lie several greatly coiled *seminiferous tubules*, *a*, *a*, averaging in length 0.68 meter (27 inches) and in diameter only 0.14 mm. ($\frac{1}{180}$ inch). Their total number in each gland is about 800. Near the posterior side of the testis the tubules unite to form about 20 *vasa recta* (*b*), and these pass out of the gland at its

upper end, as *the vasa efferentia* (*d*), which become coiled up into conical masses, the *coni vasculosi;* these, when unrolled, are tubes from 15 to 20 cm. (6–8 inches) in length; they taper somewhat from their commencements at the vasa efferentia, where they are 0.5 mm. ($\frac{1}{50}$ inch) in diameter, to the other end where they terminate in the *epididymis* (*e, e,* Fig. 156). The latter is a narrow mass, slightly longer than the testicle, which lies along the posterior side of that organ, near the lower end of which it passes (*g*) into the *vas deferens, h.* If the epididymis be carefully unraveled it is found to consist of a tube about 6 meters (20 feet) in length, and varying in diameter from 0.35 to 0.25 mm. ($\frac{1}{70}$ to $\frac{1}{90}$ inch).

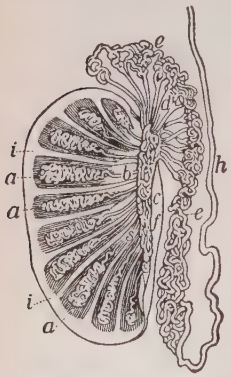


Fig. 156.—Diagram of a vertical section through the testis. *a, a,* tubuli seminiferi; *b,* vasa recta; *d,* vasa efferentia ending in the coni vasculosi; *e, e,* epididymis. *h,* vas deferens.

The *vas deferens* (*h,* Fig. 156) commences at the lower part of the epididymis as a coiled tube, but it soon ceases to be convoluted and passes up beneath the skin covering the inner part of the groin, till it gets above the pelvis and then, passing through the abdominal walls, turns inwards, backwards, and downwards, to the underside of the urinary bladder, where it joins the duct of the seminal vesicle; it is about 0.6 meter (2 feet) in length and 2.5 mm. ($\frac{1}{10}$ inch) in diameter. Its lining epithelium is ciliated.

The *vesiculæ seminales,* two in number, are membranous receptacles which lie, one on each side, beneath the bladder, between it and the rectum. They are commonly about 5 cm. (2 inches) long and a little more than a centimeter wide (or about 0.5 inch) at their broadest part. The narrowed end of each enters the vas deferens on its own side, the tube formed by the union being the *ejaculatory duct,* which, after a course of about an inch, enters the urethra near the neck of the bladder. In some animals the *vesiculæ seminales* form a liquid which is added to the secretion of the testis. In man they appear to be merely reservoirs in which the semen collects.

The *prostate gland* is a dense body, about the size of a large cherry, which surrounds the commencement of the urethra; the ejaculatory ducts pass through it. It is largely made up of fibrous and unstriped muscular tissues, but contains also a num-

ber of small secreting saccules whose ducts open into the urethra. The prostatic secretion though small in amount would appear to be of importance: at least the gland remains undeveloped in persons who have been castrated in childhood; and atrophies after removal of the testicles later in life.

The *male urethra* leads from the bladder to the end of the penis, where it terminates in an opening, *the meatus urinarius*. It is described by anatomists as made up of three portions, the prostatic, the membranous, and the spongy. The first is surrounded by the prostate gland and receives the ejaculatory ducts. On its posterior wall, close to the bladder, is an elevation containing erectile tissues (see below) and supposed to be dilated during sexual congress, so as to cut off the passage to the urinary receptacle. On this crest is an opening leading into a small recess, the *utricle*, which is of interest, since the study of its embryology shows it to be an undeveloped male uterus. The succeeding membranous portion of the urethra is about 1.8 cm. ($\frac{3}{4}$ inch) long; the spongy portion lies in the penis.

The *penis* is composed mainly of *erectile tissue*, *i. e.*, tissues so arranged as to inclose cavities which can be distended by blood. Covered outside by the skin, internally it is made up of three elongated cylindrical masses, two of which, the *corpora cavernosa*, lie on its anterior side; the third, the *corpus spongiosum*, surrounds the urethra and lies on the posterior side of the organ for most of its length; it, however, alone forms the terminal dilation, or *glans*, of the penis. Each *corpus cavernosum* is closely united to its fellow in the middle line and extends from the pubic bones, to which it is attached behind, to the glans penis in front. It is enveloped in a dense connective-tissue capsule from which numerous bars, containing white fibrous, elastic, and smooth muscular tissues, radiate and intersect in all directions, dividing its interior into many irregular chambers called *venous sinuses*. Into these blood is conveyed partly through open capillaries, partly directly by the open ends of small arteries; this blood is carried off by veins proceeding from the sinuses.

The arteries of the penis are supplied with vasodilator nerves, (p. 395), derived from the sacral plexus. Under certain conditions these are stimulated and, the arteries expanding, blood is poured into the venous sinuses faster than the veins

drain it off; the latter are probably also at the same time compressed where they leave the penis by the contraction of certain muscles passing over them. Simultaneously the involuntary muscular tissue of the bars ramifying through the erectile masses relaxes. As a result the whole organ becomes distended and finally rigid and erect. The co-ordinating *center of erection* lies in the lumbar region of the spinal cord, and may be excited reflexly by mechanical stimulation of the penis, or under the influence of nervous impulses originating in the brain and associated with sexual emotions. The corpus spongiosum resembles the corpora cavernosa in essential structure and function.

The skin of the penis is thin and forms a simple layer for some distance; towards the end of the organ it separates and forms a fold, the *foreskin* or *prepuce*, which doubles back, and, becoming soft, moist, red, and very vascular, covers the glans to the *meatus urinarius*, where it becomes continuous with the mucous membrane of the urethra; in it, near the projecting posterior rim of the glans, are imbedded many sebaceous glands. It possesses nerve end organs (*genital corpuscles*) which are undoubtedly receptors of tactile sense.

The Seminal Fluid. The essential elements of the testicular secretion are much modified cells, the *spermatozoa*, which are passed out wth some albuminous liquid. The spermatozoa (Fig. 157) are motile bodies about 0.04 mm. ($\frac{1}{500}$ inch) in length. They have a flattened clear *body* or *head* and a long vibratile *tail* or cilium; the portion of the tail nearest to the head is thicker than the rest, and is known as the *neck*. The mode of development of a spermatozoön shows that the head is a cell-nucleus and the neck and tail a modified cell-body.

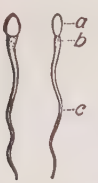


FIG 157.—Spermatozoa, seen from the front and inside view. *a*, head; *b*, neck; *c*, tail.

On cross-section a seminiferous tubule presents externally a well-marked basement membrane, upon which are borne several layers of cells; the lumen or bore of the tubule is in great part occupied by the tails of spermatozoa projecting from some of the lining cells. The outer cells, those next the basement membrane, are arranged in a single layer, and are usually found in one or other stage of active mitosis (p. 594). The result of the division is an outer cell, which remains next the basement mem-

brane to repeat the process, and an inner, which is the *mother-cell* of spermatozoa. The latter by the process of maturation described in a former paragraph (p. 595) gives rise to four cells each of which develops into a functional spermatozoön.

The Reproductive Organs of the Female. Each ovary (*o*, Fig. 158) is a dense oval mass about 3.25 cm. (1.5 inches) in length, 2 cm. (0.75 inch) in width, and 1.27 cm. (0.5 inch) in thick-

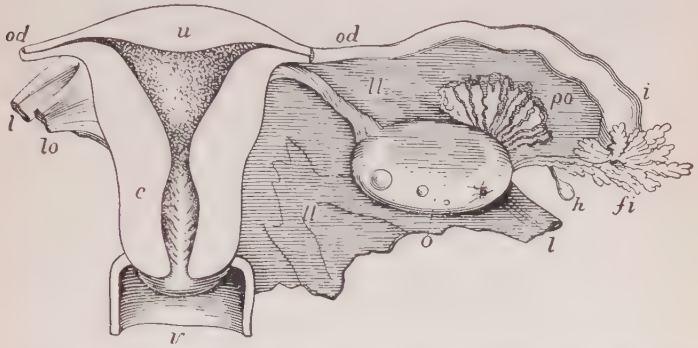


FIG. 158.—The uterus, in section, with the right Fallopian tube and ovary, as seen from behind, about $^2/_3$ the natural size. *u*, upper part of uterus; *c*, cervix; *v*, upper part of vagina; *od*, Fallopian tube; *fi*, its fimbriated extremity; *o*, ovary; *po*, parovarium.

ness; it weighs from 4 to 7 grams (60–100 grains). The organs lie in the pelvic cavity enveloped in a fold of peritoneum (the *broad ligament*), and receive blood vessels and nerves along one border. From time to time ova reach the surface, burst through the enveloping peritoneum, and are received by the wide fringed aperture, *fi*, of the oviduct or Fallopian tube, *od*. This tube narrows towards its inner end, where it communicates with the uterus, and is lined by a mucous membrane, covered by ciliated epithelium; plain muscular tissue is also developed in its wall. The *uterus* (*u*, *c*, Fig. 158) is a hollow organ, with relatively thick muscular walls (left unshaded in the figure); it contains the fetus during pregnancy and expels it at birth; it lies in the pelvis between the urinary bladder and the rectum (Fig. 159); the Fallopian tubes open into its anterior corners. It is free above, but its lower end is attached to and projects into the vagina. In the fully developed virgin state the organ is somewhat pear-shaped, but flattened from before

back; about 7.5 cm. (3 inches) in length, 5 cm. (2 inches) in breadth at its upper widest part, and 2.5 cm. (1 inch) in thickness; it weighs from 25 to 42 grams ($\frac{7}{8}$ to $1\frac{1}{2}$ oz.). The upper wider portion of the womb is known as its *body;* the cavity of this is produced at each side to meet the openings of the Fallopian tubes, and narrows below to the *neck*, or *cervix uteri*, opposite *c* (Fig. 158), the com-

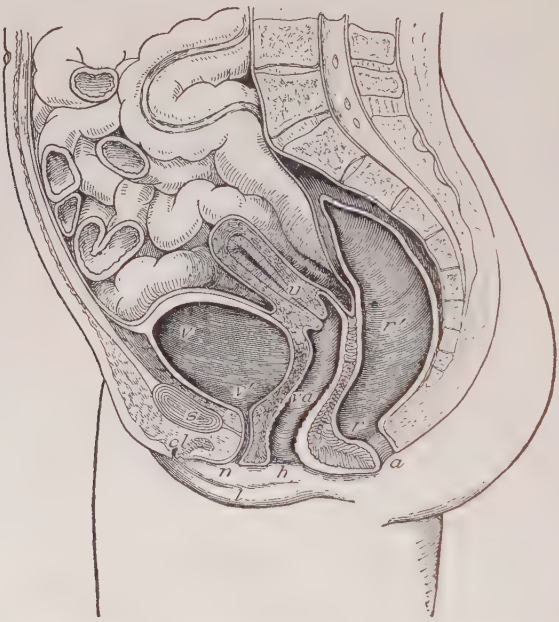


Fig. 159.—The viscera of the female pelvis as exposed by a dorsiventral median section. *s*, symphysis pubis; *v*, *v'*, urinary bladder; *u*, urethra; *u*, uterus; *va*, vagina; *r*, *r'*, rectum; *a*, anal opening; *l*, right labium major; *n*, right nympha; *h*, hymen; *cl*, divided cilitoris.

munication between neck and body cavities being known as the *os internum*. Below this the neck dilates somewhat: it forms no part of the cavity in which the embryo is retained and nourished. The lowest part of the cervix reaches into the vagina and communicates with it by a transverse aperture, the *os uteri*. During *gestation* or *pregnancy* the fetus develops in the body of the womb, which becomes greatly enlarged and rises high into the abdomen: the virgin womb lies mainly below the level of the bones of the pelvis.

The chief bulk of the non-gravid uterus consists of a coat of plain muscular tissue, arranged in a thin outer longitudinal layer, and an inner, thicker, consisting of oblique and circular fibers. Between the layers is an extensive vascular network, with many dilated veins or venous sinuses. The muscular coat is lined internally by a ciliated mucous membrane, and is covered externally by the peritoneum, bands of which project from each side of it as the *broad ligaments* (*ll*, Fig. 158). The outer layer of the mucous membrane presents a very well developed *muscularis mucosæ*, much thicker than the corresponding layer in the gastric or intestinal mucous membranes and much less sharply marked off from the true muscular coat outside it. The main thickness of the mucous membrane consists of closely set, simple or slightly branched, tubular glands; between these is a close blood-vascular and lymphatic network. The glands open on the interior of the womb; they and the mucous membrane between their mouths are lined by a single layer of columnar ciliated cells, with some goblet cells between them. In the cervix the glands are shorter, and many of the epithelial cells not ciliated. The viscid mucus secreted by the uterine glands is alkaline or neutral.

The *vagina* is a distensible passage, extending from the uterus to the exterior; dorsally it rests on the rectum, and ventrally is in contact with the bladder and urethra. It is lined by mucous membrane, the epithelium of which is much like the epidermis but thinner; outside the mucous membrane the vagina is made up of areolar, erectile, and unstriped muscular tissues. Around its lower end is a ring of striated muscular tissue, the *sphincter vaginæ*.

The *vulva* is a general term for all the portions of the female generative organs visible from the exterior. Over the front of the pelvis the skin is elevated by adipose tissue beneath it, and forms the *mons Veneris*. From this two folds of skin (*l*, Fig. 159), the *labia majora*, extend downwards and backwards on each side of a median cleft, beyond which they again unite. On separating the labia majora a shallow *genito-urinary sinus*, into which the urethra and vagina open, is exposed. At the upper portion of this sinus lies the *clitoris*, a small and very sensitive erectile organ, resembling a miniature penis in structure, except that it has no corpus spongiosum and is not traversed by the urethra. From the clitoris de-

scend two folds of mucous membrane, the *nymphæ* or *labia interna*, between which is the *vestibule*, a recess containing above the opening of the short femal eurethra, and below, the aperture of the vagina, which is in the virgin more or less closed by a thin duplicature of mucous membrane, the *hymen*.

Microscopic Structure of the Ovary. The main mass of the ovary consists of a dense connective-tissue *stroma*, containing unstriped muscle, blood vessels, and nerves: it is covered externally by a peculiar *germinal epithelium*, and contains imbedded in it many minute cavities, the *Graafian follicles*, in which *ova* lie. If a

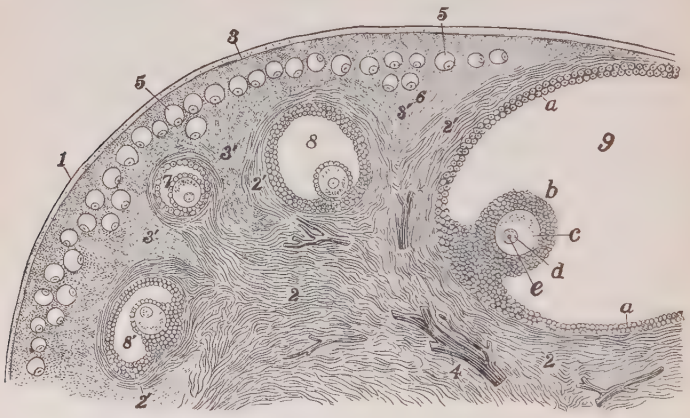


Fig. 160.—A section of a Mammalian ovary, considerably magnified. 1, outer capsule of ovary; 2, 3, 3′, stroma; 4, blood-vessels; 5, rudimentary Graafian follicles; 6, 7, 8, follicles beginning to enlarge and mature, and receding from the surface; 9, a nearly ripe follicle which is extending towards the surface preparatory to discharging the ovum; *a*, membrana granulosa; *b*, discus proligerus; *c*, ovum, with *d*, germinal vesicle, and *e*, germinal spot. The general cavity of the follicle (in which 9 is printed) is filled with lymph-like transudation liquid during life.

thin section of an ovary be examined with the microscope many hundreds of small Graafian follicles, each about 0.25 mm. ($\frac{1}{100}$ inch) in diameter, will be found imbedded in it near the surface. These are lined by cells, and each contains a single ovum. In a woman of child-bearing age there will be found also, deeper in, larger follicles (7, 8, 9, Fig. 160), their cavities being distended, during life, by liquid; in these the essential structure may be more readily made out. Each has an external fibrous coat constituted by a dense and vascular layer of the ovarian stroma; within this come several layers of lining cells (9, *a*, Fig. 160) constituting the *membrana granulosa*. At one point, *b*, the cells of this layer are

heaped up, forming the *discus proligerus*, which projects into the liquid filling the cavity of the follicle. Buried among the cells of the discus proligerus the ovum, *c*, lies.

The Mammalian Ovum. As the Graafian follicles enlarge the ova grow but not proportionately, so that they occupy relatively less of the cavities of the larger follicles: the cells of the discus proligerus probably elaborate food for the egg-cell from material derived from the blood vessels which form a close network around most of each enlarging Graafian follicle and transude crude nutritive matter into the liquid filling most of the follicle. The fully formed ovum (Fig. 161) is about 0.2 mm. ($\frac{1}{120}$ inch) in diameter: it has a well-marked outer coat or sac, *a*, the *zona radiata*, *zona pellucida* or *vitelline membrane*, surrounding a very granular *cell-body* or *vitellus*, *b*, in which is a conspicuous *nucleus*, *c*, with its characteristic network of chromatin. The main bulk of the vitellus or yolk consists of highly refracting spheroidal particles of nutritive matter (deutoplasm) imbedded in and concealing a true protoplasmic reticulum. In the eggs of birds and reptiles the deutoplasm is in very large amount and forms nearly all the yolk, the protoplasm being for the most part aggregated around the nucleus at a small area on one side of the yolk. It is in this area that new cell-formation occurs and the embryo is built up, the rest of the yolk being gradually absorbed by it; such eggs are known as *mesoblastic* or partly dividing eggs. In all the higher mammalia the deutoplasm is relatively sparse and tolerably evenly mingled with the protoplasm, and the whole fertilized ovum divides to form the first cells of the embryo: such eggs are named *holoblastic*.

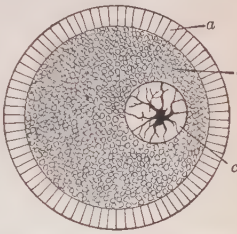


FIG. 161. — A human ovum; highly diagrammatic. *a*, zona radiata; *b*, vitellus or yolk; *c*, nucleus.

Ovulation. From puberty, during the whole child-bearing period of life, certain comparatively very large Graafian follicles may nearly always be found either close to the surface of the ovary or projecting on its exterior. These, by accumulation of liquid within them, have become distended to a diameter of about 4 mm. ($\frac{1}{6}$ inch). At quite regular intervals (varying in different species of animals from once in four days in rats to once a year in fur seals, cattle, and many other large mammals), in the human species of

once in four weeks, the thinned projecting portion of the wall of the follicle, which differs from the rest in containing few blood vessels, gives way and the ovum is discharged, accompanied by some cells of the discus proligerus. The two ovaries presumably alternate in this action, each discharging an ovum about once in eight weeks. The emptied follicle becomes filled up with a reddish-yellow mass of cells, and constitutes the *corpus luteum*, which recedes again to the interior of the ovary and begins to retrograde in 12–14 days, unless pregnancy occur; in that case the corpus luteum increases for a time, and persists during the greater part of the gestation period.

The discharged ovum enters the Fallopian tube and passes down it to the uterus. Just how the passage from the ovary to the tube occurs is not clear, although it is suggested that the cilia which line the tube set up by their motion a current sufficient to convey the ovum across the intervening space and into its mouth. Having entered the Fallopian tube the egg slowly passes on to the uterus, moved by the cilia lining the oviduct; its descent probably takes about four or five days; if not fertilized, it dies and is passed out.

In practically all mammals except human beings and apes the above process, known as *ovulation*, is attended with sexual excitement and usually other manifestations, the whole making up so-called *œstrus* or heat. In these mammals impregnation occurs only then. The male is refused at all other times.

Menstruation. During the persistence of the corpus luteum following ovulation certain changes occur in the uterus, preparatory to reception of the fertilized ovum and its implantation in position for the embryo to be properly nourished during its growth. These changes come to a climax in approximately twelve days on the average in the human female, provided fertilization has not occurred meanwhile. They culminate in a breaking down of the superficial layers of the uterine mucous membrane; the material cast off is discharged along with more or less blood, constituting the *menstrual flow*, or monthly sickness. The uterine changes which culminate in menstruation are undoubtedly due to the action of a hormone produced in the corpora lutea during their period of persistence. Except during pregnancy and while suckling, menstruation occurs at about four-weekly intervals, from puberty up to about the forty-fifth year; the periods then become irregular, and finally the discharges cease; this is an indication that ovulation

has come to an end, and that the sexual life of the woman is completed. This time, the *climacteric* or "turn of life," is a critical one; various local disorders are apt to supervene, and even mental derangement.

Hygiene of Menstruation. During menstruation there is apt to be more or less general discomfort and nervous irritability; the woman is not quite herself, and those responsible for her happiness ought to watch and tend her with special solicitude, forbearance, and tenderness, and protect her from anxiety and agitation. Any strong emotion, especially of a disagreeable character, is apt to check the flow, and this is always liable to be followed by serious consequences. A sudden chill often has the same effect; hence a menstruating woman ought always to be warmly clad, and take more than usual care to avoid draughts or getting wet. At these periods, also, the uterus is enlarged and heavy, and being (as may be seen in Fig. 157) but slightly supported, and that near its lower end, it is especially apt to be displaced or distorted; it may tilt forwards or sideways (*versions of the uterus*), or be bent where the neck and body of the organ meet (*flexion*). Hence violent exercise at this time should be avoided, though there is no reason why a properly clad woman should not take moderate exercise.

The absence of the menstrual flow (*amenorrhea*) is normal during pregnancy and while suckling; and in some rare cases it never occurs throughout life, even in healthy women capable of childbearing. Usually, however, the nonappearance of the menses at the proper periods is a serious symptom, and one which calls for prompt measures. In all such cases it cannot be too strongly impressed upon women that to take drugs tending to induce the discharge is highly dangerous, except under skilled medical advice; to excite the flow, in many cases, as for example occlusion of the os uteri, or in general debility (when its absence is a conservative effort of the system), may have the most disastrous results.

Fertilization. The ovum descends the Fallopian tube rather slowly, and fertilization usually takes place during its descent. The spermatozoa are carried upward into the tube partly, perhaps, by the contractions of the muscular walls of the female cavities, but mainly by their own activity. Occasionally the ovum is fertilized before reaching the Fallopian tube and fails to enter it, giving rise to an *extra-uterine pregnancy*.

The actual process of the fertilization of the ovum has only been observed in the lower animals, but there is no doubt that the phenomena are the same in all essentials in all cases. Some of the spermatozoa penetrate the zona radiata and one of them enters the ovum. After the entrance of a single spermatozoan a membrane forms inside the zona radiata (Fig. 161) which prevents others from entering. The head of the spermatozoan, which is chiefly chromatin, becomes separated from the tail; the latter disappears, probably by absorption into the substance of the ovum. The head, now known as the *male pronucleus*, approaches the chromatin mass of the ovum, at this stage called the *female pronucleus*, and the two fuse into a single *fertilization* or *segmentation nucleus*. This process restores to the ovum the typical number of chromosomes.

Since both parents are of the same species their chromosomes are in general similar, each one in the male pronucleus having its prototype in the female pronucleus. Similar chromosomes line up side by side, forming the pairs mentioned previously (p. 593), the significant thing about the pairs being that one member of each is of paternal, the other of maternal origin.

In addition to the chromatin material the spermatozoan also brings with it the stimulus to cell division, so that immediately after the formation of the fertilization nucleus segmentation begins. In the first and subsequent divisions, which, as stated earlier, are by the process of mitosis, the chromatin is so distributed that each daughter-cell receives equal amounts from ovum and sperm.

Heredity. The relative influence of the two parents upon the characteristics of the offspring has been studied and speculated upon for ages. With the discovery of the chromosomes it has become evident that to them we must look largely, if not wholly, for the agency of hereditary transmission. So far as paternal characters impress themselves they must do so through the chromosomes since the sperm contributes virtually nothing else. To the Austrian monk Mendel and the Dutch botanist DeVries we owe the foundations of the conception of heredity which has clarified our ideas on the subject more than all previous work has done. The principles are often referred to as "Mendelian" to commemorate the work of the first man to grasp them and bring evidence in their support.

Recalling that the genes are the actual determiners of hereditary traits, and the chromosomes aggregates of genes; and furthermore that the chromosomes form pairs of which one member is contributed by each parent, we can begin to develop a picture of the mechanism of heredity. Note that if the two parents were exactly alike in every hereditary trait, a condition not realizable in nature, all the genes contributed by the father would be matched by exactly similar genes of maternal origin; hence one chromosome of each pair would be an exact duplicate of its mate, and all hereditary traits in the offspring would have an equal impetus from each parent. The race is so mixed, as the result of long ages of interbreeding of different stocks, that instead of this ideal condition existing, the "paternal" genes are likely to differ considerably from the "maternal." For example, the father may contribute genes tending to cause the hair to be red, while the genes from the mother would lead to the development of black hair. When such a conflict of genes exists the offspring is technically a *hybrid*, in respect to the traits not in harmony. The result of such conflict may be either complete dominance of one, the character of the offspring being that of the parent contributing the dominant gene, and the other gene being "recessive," or there may be a blending of the two characters into an intermediate appearance. An example of dominance is afforded by eye-color; dark eyes are dominant over blue; on the other hand, skin pigmentation shows blended inheritance, as shown in the skin-color of mulattoes. Even though the recessive traits are not apparent in the presence of dominant conflicting characters the chromosomes which determine them persist unchanged, and will be found in the germ-cells.

When "reduction division" occurs at maturation (p. 595), the pairs of chromosomes separate and migrate to opposite poles, and so come to lie in different daughter-cells. The result is that after maturation any given germ-cell may contain either the genes for the dominant character or those for the recessive, but not both. This principle of "the purity of the germ-cell" is the corner stone of Mendelian inheritance. When such hybrids mate it is evident that there are four possible combinations of germ-cells that may occur. If we designate the dominant by D and the recessive by R, the maternal germ-cell by m and the paternal by p, we may represent the four possible combinations thus $Dm + Dp$; $Dm +$

Rp; Rm + Dp; Rm + Rp. Of these four the first and last are pure; the second and third are hybrid. Since the dominant character is present in the hybrids they will have the same appearance as number 1, which is pure dominant. Number 4, however, which is pure recessive, will have the appearance characteristic of the recessive trait. A simple illustration is furnished by eye color. Brown eyes are dominant and blue eyes recessive. According to the principles just stated brown-eyed persons may be pure dominant or hybrid, but all blue-eyed persons are pure recessive. If both parents are blue-eyed all the offspring must therefore be blue-eyed also. If both parents are brown-eyed the eye color of the offspring will depend on whether the parents are pure dominant or hybrid. If one or both are pure dominant all offspring will have brown eyes. If both are hybrid one in four of the offspring may have blue eyes.

Various things that may happen in the germ-cells, prior to the separation of the paired chromosomes, may modify the course of events; thus there is a stage at which the members of each pair come into close contact, allowing a "swapping" of blocks of genes (technically "crossing over"), so that genes formerly in a "maternal" chromosome are transferred to the corresponding "paternal," in exchange for an equal number taken over from the latter. The effect is to change the grouping of dominants and recessives within the chromosomes, with corresponding departures of the offspring from the combinations of traits they would otherwise have shown. In a certain percentage of cases chemical or physico-chemical changes occur in the genes of the germ-cells, apparently spontaneously, although as to that we cannot say definitely, with the result that wholly new traits appear in the offspring. This is a "mutation." Its effects may be far-reaching, in that new characters thus springing into being may, theoretically, prove superior to any existing at present. It is to be said, however, that during the relatively brief time mutations have been under investigation few, if any, that are really valuable have put in an appearance.

Sex Determination. An interesting application of the principles of Mendel is in the determination of sex. It appears that in the germ-cells of males of some species there is one less chromosome than in the cells of females of the same species. Human females, for example, have 24 pairs or 48 chromosomes and human

males 23 complete pairs and one odd chromosome, or 47 in all. In the reduction division that occurs in connection with maturation (p. 595) one of the daughter-cells formed from the division of the primary sperm-cell has thus only 23 chromosomes, while the other has 24. The subsequent division of the daughter-cells to form sperm preserves the same relation of numbers. Half of the spermatozoa, therefore, will have 23 chromosomes and the other half 24. Since the female germ-cells contain 48 chromosomes each ovum will have 24. In the fertilization of the ovum, if the penetrating sperm contains 24 chromosomes the offspring will be female; if only 23 the offspring will be male. Obviously this has little practical bearing on the problem of artificial sex determination, except in so far as it shows the futility of attempting to bring it about.

Sex-Linked Characters. The presence of a complete chromosome pair in females, represented in males by a single unpaired chromosome, has certain interesting consequences in heredity. The only one space permits us to mention here results from the fact that the unpaired chromosome (known as the X chromosome) can go in the offspring only to females, as shown above, consequently any traits transmitted from the male parent by means of this particular chromosome, cannot go to any of the male offspring. This may be illustrated by ordinary red-green color-blindness, which is, as stated formerly (p. 295), a "sex-linked" character. It is also recessive, a fact of importance in considering its appearance. If a color-blind male mates with a normal female none of the male offspring can be color-blind, since none of them can inherit the genes for the trait. None of the female offspring will be color-blind, either, since they will all inherit from the mother a dominant gene giving normal vision. They are all hybrids, however, with respect to this particular trait, hence a fraction of their male offspring are likely to receive the X chromosome (derived from the grandfather) which carries genes for color-blindness, and all such must be color-blind. Their female offspring cannot be color-blind unless one of them mates with a color-blind male, since in no other way can two X chromosomes, both carrying a recessive trait, such as this is, come together in the same fertilized ovum.

Impregnation. The fertilized ovum, which as we have seen (p. 607), receives the sperm in the Fallopian tube, continues its

descent to the uterine cavity, where preparatory changes have occurred under the influence of a hormone from the persistent corpus luteum (p. 606). It becomes implanted and begins to develop along the lines described earlier (p. 38). Although the time of ovulation is now known to be about twelve days before menstruation, it does not follow that impregnation can occur only at that period of the menstrual cycle. If sexual congress occurs within five or six days after ovulation the surviving ovum is likely to become impregnated, since about that period elapses between the rupture of the Graafian follicle and the death of the non-fertilized egg. If congress occurs at other periods of the cycle some of the sperms are likely to survive within the tubes long enough to function at the next ovulation. It is also probable that ovulations occur occasionally at irregular intervals; at any rate it is well known that pregnancy is likely to follow sexual congress at whatever part of the cycle it occurs.

When the newly fertilized ovum reaches the uterine cavity it becomes implanted there, as stated above; the mucous membrane lining the latter, instead of sloughing away, as happens when there is no fertilization, grows rapidly, forming a new, thick, very vascular lining to the womb, known as the decidua. The embryo becomes attached to this at one point, the decidua growing up around it. As pregnancy advances and the fetus grows, it bulges out into the uterine cavity and pushes before it that part of the decidua which has grown over it (the *decidua reflexa*); at about the end of the third month this coalesces with the decidua lining the opposite sides of the uterine cavity so that the two can no longer be separated. That part of the decidua (*decidua serotina*) against which the embryo is first attached subsequently undergoes a great development in connection with the formation of the placenta (see below). Meanwhile the whole uterus enlarges; its muscular coat especially thickens. At first the organ still lies within the pelvis, where there is but little room for it; it accordingly presses on the bladder and rectum (see Fig. 157) and the nerves in the neighborhood, frequently causing considerable discomfort or pain; and, reflexly, often exciting nausea or vomiting (the *morning sickness* of pregnancy). Later on, the pregnant womb escapes higher into the abdominal cavity, and although then larger, the soft abdominal walls more readily make room for it, and less discomfort is usually

felt, though there may be shortness of breath and palpitation of the heart from interference with the diaphragmatic movements. All tight garments should at this time be especially avoided; the woman's breathing is already sufficiently impeded, and the pressure may also injure the developing child. Meanwhile, changes occur elsewhere in the Body. The breasts enlarge and hard masses of developing glandular tissue can be felt in them; and there may be mental symptoms: depression, anxiety, and an emotional nervous state.

During the whole period of gestation the woman is not merely supplying from her blood nutriment for the fetus, but also, through her lungs and kidneys, getting rid of its wastes; the result is a strain on her whole system which, it is true, she is constructed to bear and will carry well if in good health, but which is severely felt if she be feeble or suffering from disease. The healthy married woman who endeavors to evade motherhood because she thinks she will thus preserve her personal appearance, or because she dislikes the trouble of a family, deserves but little sympathy; she is trying to escape a duty voluntarily undertaken, and owed to her husband, her country, and her race; but she whose strength is undermined and whose life is made one long discomfort for the sexual gratification of her husband deserves every consideration, and the family physician ought perhaps to warn the husband more frequently than he does of the risk to a delicate wife's health, or even life, of inordinate sexual indulgence: and the husband should control himself accordingly.

The Intra-Uterine Nutrition of the Embryo. At first the embryo is nourished by absorption of materials from the soft vascular lining of the womb; as it increases in size this is not sufficient, and a new organ, the *placenta*, is formed for the purpose. A fetal outgrowth, the *allantois*, plants itself firmly against the *decidua serotina*, and villi developed on it burrow from its surface into the uterine mucous membrane. In the deeper layer of this latter are large sinuses through which the maternal blood flows, and into which the allantoic villi project. Blood is brought from the fetus to the allantois by arteries and carried back by veins after traversing the capillaries of the villi, and while flowing through these receives, by dialysis, oxygen and food materials from the maternal blood, and gives up to it carbon dioxid, urea, and other wastes.

There is thus no direct intermixture of the two bloods; the embryo is from the first an essentially separate and independent organism. The allantois and decidua serotina becoming inseparably united together form the placenta, which in the human species is, when fully developed, a round thick mass about the size of a large saucer, connected to the embryo by a narrow stalk, the *umbilical cord*, in which blood vessels run to and from the placenta.

Parturition. At the end of from 275 to 280 days from fertilization of the ovum (*conception*) pregnancy terminates, and the child is expelled by powerful contractions of the uterus, assisted by those of the muscles in the abdominal walls. When the child is born, it has attached to its navel the umbilical cord, which is then usually ligatured and cut across. Shortly after the birth of the child renewed uterine contractions detach and expel the placenta, both its fetal or allantoic and maternal or decidual part, as the *afterbirth*. Where it is torn loose from the uterine wall large blood sinuses are left open; hence a certain amount of bleeding occurs, but in normal labor this is speedily checked by firm contraction of the uterus. Should this fail to take place profuse hemorrhage occurs (*flooding*) and the mother may bleed to death in a few minutes unless prompt measures are adopted.

For a few days after delivery there is some discharge (the *lochia*) from the uterine cavity: the whole decidua being broken down and carried off, to be subsequently replaced by new mucous membrane. The muscular fibers developed in the uterine wall in such large quantities during pregnancy undergo rapid fatty degeneration and are absorbed, and in a few weeks the organ returns almost to its original size. The parturient woman is especially apt to take infectious diseases; and these, should they attack her, are fatal in a very large percentage of cases. Very special care should therefore be taken to keep all contagion from her.

There is a current impression that a pregnancy, once commenced, can be brought to a premature end, especially in its early stages, without any serious risk to the woman. That belief is erroneous. Premature delivery, early or late in pregnancy, is always more dangerous than natural labor at the proper term; the physician has sometimes to induce it, as when a malformed pelvis makes normal parturition impossible, or the general derangement of health accompanying the pregnancy is such as to threaten the

mother's life; but the occasional necessity of deciding whether it is his duty to procure an abortion is one of the most serious responsibilities he meets with in the course of his professional work.

The production of abortion, even in the first stages of pregnancy, by the taking of drugs, the so-called *abortifacients*, a practice which from time to time has gained considerable headway through the widespread advertisement of their wares by unscrupulous vendors of "patent medicines," is so dangerous to the health, and even the life, of the woman who practices it that no consideration sanctions it.

Lactation. The mammary glands for several years after birth remain small, and alike in both sexes. Towards puberty they begin to enlarge in the female, and when fully developed form in that sex two rounded eminences, the *breasts*, placed on the thorax. A little below the center of each projects a small eminence, the *nipple*, and the skin around this forms a colored circle, the *areola*. In virgins the areolæ are pink; they darken in tint and enlarge during the first pregnancy and never quite regain their original hue. The mammary glands are constructed on the compound racemose type. Each consists of from fifteen to twenty distinct lobes, made up of smaller divisions; from each main lobe a separate *galactophorous duct*, made by the union of smaller branches from the lobules, runs towards the nipple, all converging beneath the areola. There each dilates and forms a small elongated reservoir in which the milk may temporarily collect. Beyond this the ducts narrow again, and each continues to a separate opening on the nipple. Imbedding and enveloping the lobes of the gland is a quantity of firm adipose tissue which gives the whole breast its rounded form.

During maidenhood the glandular tissue remains imperfectly developed and dormant. Early in pregnancy it begins to increase in bulk, and the gland-lobes can be felt as hard masses through the superjacent skin and fat. Even at parturition, however, their functional activity is not fully established. The oil-globules of the milk are formed by a sort of fatty degeneration of the gland-cells, which finally fall to pieces; the cream is thus set free in the watery and albuminous secretion formed simultaneously, while newly developed gland-cells take the place of those destroyed. In the milk first secreted after accouchement (the *colostrum*) the

cell destruction is incomplete, and many cells still float in the liquid, which has a yellowish color; this first milk acts as a purgative on the infant, and probably thus serves a useful purpose, as a certain amount of substances (biliary and other), excreted by its organs during development, are found in the intestines at birth.

Human milk is undoubtedly the best food for an infant in the early months of life; and to suckle her child is useful to the mother if she be a healthy woman. Many women refuse to suckle their children from a belief that so doing will injure their personal appearance, but skilled medical opinion is to the contrary effect; the natural course of events is the best for this purpose, unless lactation be too prolonged. Of course in many cases there are justifiable grounds for a mother's not undertaking this part of her duties; a physician is the proper person to decide.

In a healthy woman, not suckling her child, ovulation and menstruation recommence about six weeks after childbirth; a nursing mother usually does not menstruate for ten or twelve months; the infant should then be weaned.

When an infant cannot be suckled by its mother or a wet-nurse an important matter is to decide what is the best food to substitute. Good cow's milk contains rather more fats than that of a woman, and much more casein; the following table gives averages in 1,000 parts of milk:

	Woman	Cow
Casein	28.0	54.0
Butter	33.5	43.0
Milk-sugar	44.5	42.5
Inorganic matters	4.75	7.75

The inorganic matters of human milk yield, on analysis, in 100 parts—calcium carbonate, 6.9; calcium phosphate, 70.6; sodium chlorid, 9.8; sodium sulphate, 7.4; other salts, 5.3. The lime salts are of especial importance to the child, which has still to build up nearly all its bony skeleton.

When undiluted cow's milk is given to infants they rarely bear it well; the too abundant casein is vomited in loose coagula. The milk should therefore be diluted with half or, for very young children, even two-thirds its bulk of water. This, however, brings down the percentage of sugar and fat below the proper amount.

The sugar is commonly replaced by adding cane-sugar; but sugar of milk is readily obtainable and is better for the purpose. If used at all it should, however, be employed from the first; it sweetens much less than cane-sugar, and infants used to the latter often refuse milk in which milk-sugar is substituted. In order to bring the percentage of fat up to normal it is usual to dilute, not "whole milk" but "top milk." The latter, after the milk has stood for a few hours, contains enough of the rising cream to supply the needed fat. As the infant grows older less diluted cow's milk may gradually be given; after the seventh or eighth month no water need be added.

It should not be necessary to emphasize the vital importance of giving to infants only the purest milk obtainable. It is unfortunately true that the milk produced in many dairies is not only dirty but swarming with micro-organisms. In cities it has become the practice for medical societies to inspect various dairies and set their seal of approval upon those that fulfill the sanitary conditions essential to the production of pure, clean milk. The slightly higher cost of such "certified" milk should not be allowed to bar it from homes where children are to be fed except where extreme poverty makes its procurement impossible. In small towns and in the country personal inspection of the source of the milk supply on the part of parent or physician should give assurance of its cleanliness. Where it is impossible to procure milk free from suspicion, *pasteurization* (heating to 120° F. for 20 minutes) should be resorted to. This destroys most of the dangerous organisms, but of course is not a complete substitute for cleanliness and care in the production of the milk in the beginning.

In the first weeks after birth it is no use to give an infant starchy foods, as arrowroot. The greater part of the starch passes through the bowels unchanged; apparently because the pancreas has not yet fully developed, and has not commenced to make its starch-converting enzym. Later on, starchy substances may be added to the diet with advantage, but it should be borne in mind that they cannot form the chief part of the child's food: it needs proteins for the formation of its tissues, and carbohydrate foods contain none of these. Some infants are, ignorantly, half starved by being fed almost entirely on such things as cornflour or arrowroot.

Puberty. The condition of the reproductive organs of each sex described in preceding pages is that found in adults; although mapped out, and, to a certain extent, developed before birth and during childhood, these parts grow but slowly and remain functionally incapable during the early years of life; then they comparatively rapidly increase in size and become physiologically active; the boy or girl becomes man or woman.

This period of attaining sexual maturity, known as puberty, takes place from the eleventh to the sixteenth year, and is accompanied by changes in many parts of the Body. Hair grows more abundantly on the pubes and genital organs, and in the armpits, in the male also on various parts of the face. The lad's shoulders broaden; his larynx enlarges, and lengthening of the vocal cords causes a fall in the pitch of his voice; all the reproductive organs increase in size; fully formed seminal fluid is secreted, and erections of the penis occur. As these changes are completed spontaneous nocturnal seminal emissions take place from time to time during sleep, being usually associated with voluptuous dreams. Many a young man is alarmed by these; he has been kept in ignorance of the whole matter, is too bashful to speak of it, and getting some quack advertisement thrust into his hand in the street is alarmed to learn that his strength is being drained off, and that he is on the highroad to idiocy and impotence unless he place himself in the hands of the advertiser. Lads at this period of life should have been taught that such emissions, when not too frequent and not excited by any voluntary act of their own, are natural and healthy. They may, however, occur too often; if there is any reason to suspect this, the family physician should be consulted, as the healthy activity of the sexual organs varies so much in individuals as to make it impossible to lay down numerical rules on the subject. The best preventives in any case are, however, not drugs, but an avoidance of too warm and soft a bed, plenty of muscular exercise, and keeping out of the way of anything likely to excite the sexual instincts.

In the woman the pelvis enlarges considerably at puberty, and commonly, more subcutaneous adipose tissue develops over the Body generally, but especially on the breasts and hips; consequently the contours become more rounded. The external generative organs increase in size, and the clitoris and nymphæ become

erectile. The uterus grows considerably, the ovaries enlarge, some Graafian follicles ripen, inducing ovulation, and menstruation commences.

Hormones of the Reproductive System. The interrelations of various processes in the functioning of the reproductive mechanism are many of them very striking and they have long been the subject of investigation. The development of the so-called *secondary sexual characters* at puberty, where in a few weeks the vocal cords change and hair develops over various parts of the body, is a good example of the sort of interrelations that occur in this system. The fact, known for centuries, that castration in early life prevents the appearance of the secondary sexual characters, shows that they are directly dependent on the reproductive organs. Before the idea of hormone action had crystallized to its present form some such mechanism had been postulated for the reproductive system. For it is difficult to explain such effects as those of castration on any other basis than that the generative organs elaborate some control-exercising substance of which the body is deprived by castration. Interesting examples of hormones concerned with reproduction are those that have to do with lactation. It has been proven that the functional development of the mammary glands during pregnancy is caused by a hormone produced in the body of the embryo. This hormone is attended apparently by another one, which, while permitting the development of the glands inhibits their active functioning. At the birth of the child this second hormone is withdrawn, and the glands are thus left free to pour forth their secretion.

The Stages of Life. Starting from the ovum each human being runs through a life-cycle which terminates on the average, if not interrupted by disease or accident, after a course of from 75 to 80 years. The earliest years are marked not only by rapid growth but by differentiating growth or *development;* then comes a more stationary period, and finally one of degeneration. The life of various tissues and of many organs is not, however, coextensive with that of the individual. At birth numerous bones are represented mainly by cartilage. The pancreas has not attained its full development; and some of the sense-organs seem to be in the same case; at least new-born infants appear to hear very imperfectly. The reproductive organs only attain

full development at puberty, and degenerate and lose all or much of their functional importance as years accumulate. Certain organs have a still shorter range of physiological life; the thymus, for example, attains its fullest development at the end of the second year and then gradually dwindles away, so that in the adult scarcely a trace of it is to be found. The milk-teeth are shed in childhood, and their so-called permanent successors rarely last to ripe old age.

During early life the Body increases in mass, at first very rapidly, and then more slowly, till the full size is attained, except that girls make a sudden advance in this respect at puberty. Henceforth the woman's weight (excluding exceptional cases of accumulation of non-working adipose tissue) remains about the same until the climacteric. After that there is often an increase of weight for several years due mainly to increased formation of fat; a man's weight usually slowly increases until forty.

As old age comes on a general decline sets in, the rib cartilages become calcified, and lime salts are laid down in the arterial walls, which thus lose their elasticity; the refracting media of the eye become more or less opaque; the physiological irritability of the sense-organs in general diminishes; and fatty degeneration, diminishing their working power, occurs in many tissues. In the brain we find signs of less plasticity; the youth is ready to accept novelties and form new associations; but the longer he lives, the more difficult does this become to him. A man past middle life may do good, or even his best work, but almost invariably in some line of thought which he has already accepted; it is extremely rare for an old man to take up a new study or change his views, philosophical, scientific, or other. Hence, as we live, we all tend to lag behind the rising generation.

Death. After the prime of life the tissues dwindle (or at least the most important ones) as they increased in childhood.

Before any great diminution takes place, however, a breakdown occurs somewhere, the enfeebled community of organs and tissues forming the man is unable to meet the contingencies of life, and death supervenes. "It is as natural to die as to be born," Bacon wrote long since; but though we all know it, few realize the fact until the summons comes. To the popular imagination the prospect of dying is often associated with thoughts of extreme suf-

fering; personifying life, men picture a forcible and agonizing rending of it, as an entity, from the bodily frame with which it is associated. As a matter of fact, death is probably rarely associated with any immediate suffering. The sensibilities are gradually dulled as the end approaches; the nervous tissues, with the rest, lose their functional capacity, and, before the heart ceases to beat, the individual has commonly lost consciousness.

The actual moment of death is hard to define: that of the Body generally, of the mass as a whole, may be taken to be the moment when the heart makes its last beat; arterial pressure then falls irretrievably, the capillary circulation ceases, and the tissues, no longer nourished from the blood, gradually die, not all at one instant, but one after another, according as their individual respiratory or other needs are great or little.

While death is the natural end of life, it is not its aim—we should not live to die, but live prepared to die. Life has its duties and its legitimate pleasures, and we better play our part by attending to the fulfillment of the one and the enjoyment of the other, than by concentrating a morbid and paralyzing attention on the inevitable, with the too frequent result of producing indifference to the work which lies at hand for each. Our organs and faculties are not talents which we may justifiably leave unemployed; each is bound to do his best with them, and so to live that he may most utilize them. An active, vigorous, dutiful, unselfish life is a good preparation for death; when that time, at which we must pass from the realm controlled by physiological laws, approaches, when the hands tremble and the eyes grow dim, when "the grasshopper shall be a burden and desire shall fail," then, surely, the consciousness of having quitted us like men in the employment of our faculties while they were ours to use, will be no mean consolation.

APPENDIX

SUGGESTIONS FOR LABORATORY WORK

To a greater and greater extent colleges and normal schools are supplementing text-book instruction in Physiology with practical work in the laboratory. For such work laboratory instructions must be provided. There are upon the market numerous excellent laboratory manuals of Physiology, but most of them have been prepared for use in Medical Schools, and with the needs of Medical Students primarily in mind. The aim of this appendix is to furnish a basis for the preparation of a manual suited to the needs of students who are pursuing the subject nonprofessionally. The complete equipment of a Physiological laboratory is rather extensive, and in many cases not available in entirety. The time which can be devoted to laboratory work in Physiology varies greatly in different institutions. For these two reasons it has seemed best not to offer in this connection a manual of selected experiments, but rather to suggest simple exercises that can be adapted by the teacher to his particular requirements.

The special character of much of the work of the physiological laboratory demands a certain amount of special preparation on the part of the teacher. In describing the following experiments this preparation is assumed. The majority of teachers of Biology have it. For those who have not, and wish to introduce in their classes laboratory work in Physiology, resort may be had to one of the summer courses in Physiology now offered by the larger Universities in various parts of the country.

Fortunately for the successful development of laboratory Physiology in America the special apparatus required can be obtained of American manufacture and at a moderate price. Information as to where such apparatus may be bought can be had upon application to the department of Physiology in any of the larger Universities.

INTRODUCTION

General Histology of Body. Microscopic study of typical cells and tissues. Desirable for students who have no previous histological training.

General Chemistry of Body. *Inorganic Constituents.* Water. The percentage of water in flesh may be determined roughly by placing a weighed piece of meat in a desiccator in a warm place and weighing it at intervals until thoroughly dry.

Inorganic Salts. A weighed piece of meat may be incinerated under a hood and the ash weighed. The solubility of the ash in water may be ascertained. Tests for chlorids with silver nitrate, and for calcium with sodium oxalate solution may be applied.

Organic Constituents. Carbohydrates. *Dextrose* is present in honey and corn syrup. The test for its presence is by means of *Fehling's Solution* (see any laboratory manual of Organic Chemistry). The presence of a reddish precipitate in the test tube in which mixed Fehling's solution (alkaline copper tartrate) and dextrose are combined and heated to boiling is the test.

Glycogen is a constituent of oysters. Grind a raw oyster with sand in a mortar. Extract with water. Add to a few drops of the juice in a test tube a few drops of iodin solution (tincture may be used). A mahogany-brown color is the test for glycogen.

Lactose. If sweet milk is clotted with rennet and filtered the whey contains milk sugar. Test with Fehling's solution as for dextrose.

Fats. *Solubility of Fats.* Shake a small piece of lard with some ether in a test tube. Pour some of the solution on filter paper and allow it to evaporate. If the ether dissolved the fat, a grease spot will be left on the filter paper after the evaporation of the ether.

Moisten a second filter paper with ether, allow it to evaporate. Compare the two filter papers. The test may be repeated with olive oil instead of lard.

Test for Fats. Melt a small piece of lard in a test tube and to it add a drop of dilute osmic acid. This acid turns fat black.

Composition of Fats. Fats are compounds of fatty acids with glycerol. To separate the constituents heat on a water bath a

small piece of lard with an alcoholic solution of caustic potash. After forty minutes pour the mixture into a dish containing 100 c. c. water. Drive off the alcohol by heating over water. While still hot acidify with sulphuric acid. On cooling the fatty acid forms a solid crust on the surface of the liquid. Remove it. The glycerol is dissolved in the liquid.

The fatty acid is insoluble in water as may be shown by test.

Saponification. Soap is a compound of fatty acid with alkali. Shake some of the fatty acid produced above with warm dilute caustic soda. Filter. The filtrate shows the characteristic features of a soap solution. Soaps form an insoluble compound with calcium chlorid. This can be shown by adding a few drops of calcium chlorid to some of the soap solution in a test tube. Hard water contains calcium salts. This explains the difficulty of using soap with hard water.

Proteins. *Tests for Proteins.* Raw egg white is a satisfactory protein for these tests.

Heat Test. To a small amount of a solution of protein add a drop of a two-tenths per cent solution of acetic acid. Heat the upper portion of the solution. The protein is rendered insoluble and is now a coagulated protein.

Biuret Test. To a solution of protein add a drop or two of a one per cent solution of copper sulphate ($CuSO_4$) and then strong sodic hydrate (NaOH). A characteristic violet color is the test.

Xanthoproteic Reaction. To a solution of protein add a few drops of strong nitric acid (HNO_3), and boil; after cooling, add ammonic hydrate (NH_4OH). A yellow color which deepens to orange when the ammonia is added is the test.

Physico-Chemical Principles. *Osmosis.* Tie an osmotic membrane (gold beater's skin, bladder) across the mouth of a funnel or thistle tube. Fill with a sugar solution of the consistency of syrup. Attach a glass tube to the nozzle of the funnel. Fasten in an upright position and surround the funnel with distilled water in a beaker.

Drops of blood on a microscope slide may be used to demonstrate osmosis indirectly. Three such drops should be examined; one diluted with distilled water; a second with 0.9 per cent sodium chlorid; the third with 10 per cent sodium chlorid. Avoid excessive evaporation. The destruction of the corpuscles in the dilute solu-

tion by over-distension (*plasmolysis*); their preservation in the 0.9 per cent saline; and their shrinkage (*crenation*) in the concentrated solution illustrate osmosis.

Dialysis. Sausage casings if free from holes make good dialyzing tubes, or special tubes may be purchased from chemical supply houses. To illustrate the separation of small molecules from large by dialysis make a mixture of raw egg white with moderately concentrated sodium chlorid solution. Place in the dialyzing tube; suspend the tube in a beaker of distilled water. Stir the water frequently. After a sufficient interval the presence of sodium chlorid in the water can be demonstrated with silver nitrate, but the biuret test for protein (a very delicate test) continues negative.

THE SUPPORTING TISSUES

Gross and microscopic studies of bones and cartilage, and microscopic studies of various forms of connective tissue may be made as the time and available material permit, and as the previous training of the students requires.

That bone consists of inorganic salts deposited in an organic matrix may be shown by dissolving out the inorganic salts with dilute hydrochloric acid. That calcium is an important constituent of the inorganic portion may be shown by testing the hydrochloric acid solution with sodium oxalate.

Gelatin is a product obtained from bones by cooking them in water heated above the normal boiling point by inclosing in a sealed vessel. The ordinary protein tests applied to gelatin show that it is a member of the group of proteins.

The Skeleton

The general arrangement of the bones of the skeleton, and details of selected regions, as the skull, may be studied.

Joints. In connection with work on the skeleton the various types of joints should be studied in detail.

Typical joints are those at hip, knee, and ankle.

Hip Joint. Observe on the outer surface of the innominate bone a deep depression, the acetabulum, into which fits the smooth, nearly spherical *head* of the femur, making a *ball and socket joint.* Study the possible movements of the joint. Note (1) *flexion,*

simple bending of the joint as in walking; (2) *extension*, the opposite of flexion; (3) abduction, drawing the leg outward from the body; (4) adduction, the opposite of abduction; (5) *rotation*, twisting at the joint as in placing ankle on knee.

In addition to these elementary joint movements, the hip joint permits various combination movements, as flexion with abduction. Note these.

Knee Joint. Observe the surfaces on femur and tibia which come together at the knee. Analyze the possible movements of this joint.

Ankle Joint. Observe the possible movements of this joint.

MUSCLES

For dissection studies the cat is the most available mammal.* Detailed descriptions are given in "The Anatomy of the Cat" by Reighard and Jennings. Freshly killed animals should be used so far as possible. For temporary preservative (through two or three laboratory periods) 10–15 per cent chloral hydrate is satisfactory. For purposes of illustration directions for a single region are included here.

Dissection of Hind Leg of Cat. *Directions for dissection.* Muscles are inclosed in and bound together by sheets of connective tissue, which make up the *fascia.* To dissect out a muscle cut or tear through the fascia which joins it to its neighboring muscles until the desired muscle can be lifted clear except for the attachments at its ends. Do not cut attachments until you have finished the study of the muscle.

The attachment of the muscle nearer the trunk is called the *origin;* the attachment further from the trunk is the *insertion.*

In dissecting the hind leg of the cat, consider it as made up of four regions: pelvis, thigh, shank, and foot. The muscles are to be dissected in order as directed below. As each is cleared from its surrounding muscles the region in which it has its origin is to be determined, also the region of its insertion.

Muscles are grouped functionally, according to the joint-motions they produce, as flexors, extensors, abductors, adductors,

* If there is a pork-packing establishment in the vicinity embryo pigs can usually be obtained in ample numbers. These make exceedingly satisfactory dissection material, especially for elementary classes.

and rotators.* Determine for each muscle the region it moves and the motion it produces.

On the outside of the thigh is the *biceps femoris*. Abductor of leg and flexor of shank. Directly beneath the biceps femoris observe the large nerve, the *sciatic*.

Along the front edge of the thigh and on its inner surface is the *sartorius* or tailor's muscle. Extensor of shank, adductor of leg, and rotator of leg.

The entire mass of muscle in front of the femur after the sartorius has been removed is the *quadriceps femoris*. Extensor of shank.

On the inner surface of the thigh toward the back is the *gracilis*. Adductor of leg.

On the inner surface of the thigh after the removal of the gracilis appear the following muscles from front to back. Small *adductor longus*. Adductor of leg. The larger triangular *adductor femoris*. Extensor of thigh. Large flat *semi-membranosus*. Extensor of thigh.

After dissection of above muscles there remains on the thigh only the semi-tendinosus. Flexor of shank.

The great mass of muscle forming the calf consists of three muscles, the *plantaris*, *gastrocnemius*, and *soleus*. Do not try to separate these. The *tendo achilles* is their common tendon. Extensor of foot.

After removing above muscles there will be found against the shank bones at the back the *flexor longus digitorum*. Flexor of toes.

Along the front of the shank, a superficial muscle with its tendon toward the inner side, is the *tibialis anterior*. Flexor of foot.

Partly underneath the above, with its tendon toward the outer side, is the *extensor digitorum longus*. Extensor of toes.

The Contraction of Muscles. The tissues of cold-blooded animals are well suited for studies of function since they survive, sometimes for hours, the general death of the animal.

From the hind leg of a recently killed frog make a *femur-gastrocnemius* preparation. This preparation is used for the study of muscular contraction.

To study muscular contraction adequately the motions of the muscle must be magnified and recorded. For obtaining a magnified record of its movements the muscle is fastened in a

* Elevators, depressors, and sphincters occur in the Body but not in the leg.

clamp and its tendon attached to the short arm of a lever, whose long arm presses lightly at its tip against a smoked paper on which every movement of the muscle is recorded as a line (p. 103). To avoid superposing separate tracings the smoked paper is mounted on a drum which can be moved by hand, or driven at various speeds by a clockwork. This apparatus is called a kymograph. Tracings made with it can be preserved by passing the paper bearing them through a solution of shellac in alcohol.

Skeletal muscles contract only when stimulated. A suitable artificial stimulus is the shock from an induction coil. Induced currents are generated in the secondary coil of an inductorium when, and only when, a current is made or broken in the primary coil. An ordinary dry cell is a good source of current. The strength of the induced current varies with the position of the secondary coil relative to the primary, being greatest when the secondary is directly over the primary, and least when the secondary is withdrawn as far as possible from the primary and turned at right angles to it.

Mount the frog's gastrocnemius muscle in readiness for obtaining tracings of its contractions. By means of fine copper wires establish a circuit from the secondary coil of the inductorium through the tissue. Be careful to avoid short circuits.

With the secondary coil in the position of least effectiveness make and break the primary circuit. If the muscle does not respond shift the secondary, little by little, toward the position of greatest effectiveness, making and breaking the primary circuit with each shift. As soon as the muscle responds, recording its contraction on the smoked paper, move the drum forward by hand so that new contractions will not be superposed on the first one.

Continue increasing the strength of the shock, obtaining records of each contraction.

Thus the relation of contraction height to stimulation strength is shown.

A current is induced in the secondary at make and at break of the primary current. Determine which is a more powerful stimulus, a "make" shock or a "break" shock.

The inductorium as used in the physiological laboratory is provided with an automatic circuit breaker which can be included in

the primary circuit. Make the proper connections for doing this. Now when the circuit is closed shocks are sent into the muscle in rapid succession.

Set the clockwork of the kymograph to drive the drum at a slow speed. Obtain a tracing showing the response of the muscle to rapidly repeated stimuli. This sort of contraction is known as a *physiological tetanus* or a tetanic contraction (p. 121).

The Staircase Effect, Contracture, Fatigue. Prepare and mount a gastrocnemius muscle as in the previous exercise. Set the secondary of the inductorium at a position that gives a sharp but not excessive break stimulus. With the drum moving at its slowest speed make and break the primary circuit twice per second, allowing the contractions to record themselves on the slowly moving drum. Continue the series of stimuli until the muscle ceases to respond. Make the record permanent.

The increase in the height of the contractions during the first part of the record, due to "warming up" is called the "staircase effect."

A rise in the base line during the later part of the curve is the phenomenon of contracture (p. 119).

The final failure of the muscle to contract is the result of fatigue. This might be explained either as due to the exhaustion of the fuel supply or to the accumulation of harmful "fatigue products."

To distinguish between these alternatives replace the fatigued muscle with a fresh one. Arrange the primary circuit for rapidly repeated shocks of moderate intensity. With the muscle recording on a slowly moving drum close the key, throwing the muscle into tetanus. Continue the stimulation until the muscle is well fatigued. Let the muscle rest for five minutes. Repeat the stimulation. Recovery under this condition proves that the previous fatigue could not have been due to exhaustion of the fuel supply.

The production of acid in an active muscle may be demonstrated with sensitive litmus paper. A resting isolated muscle is neutral or slightly alkaline to litmus. The same muscle, exercised to fatigue, is acid to litmus.

The Influence of Temperature on Contraction. For this study arrangement must be made for immersing the muscle in a liquid and at the same time recording its contractions. A method of doing this is to mount an L-shaped glass rod in a clamp. Fasten

the femur end of the frog's gastrocnemius to the horizontal end of the L. A small pulley must be mounted above the rod, over which a thread can be led from the tendon of the muscle to the recording lever. Connect the ends of the muscle by fine copper wire to the terminals of the secondary coil. Set this so that the muscle gives a vigorous contraction upon stimulation. Bring around the muscle a beaker of ice-cold Ringer's solution (NaCl 0.7%; $CaCl_2$ 0.026%; KCl 0.03%), which has the same osmotic pressure as frog's blood.

With the drum moving at the fastest clockwork speed obtain a record of a single contraction.

Withdraw the cold solution and allow the muscle tissue to return to room temperature. With the drum moving at the same rate as before obtain a record of a single contraction. Now surround the muscle with Ringer's solution warmed to 30° C., and obtain a record of a single contraction, again with the drum at the same speed as before.

Let the drum make a complete revolution at the speed used in making those records. Determine as accurately as possible the time consumed. After the smoked paper has been removed measure its length, and calculate the speed of the drum in centimeters per second.

Varnish the tracings and mount side by side the records of contraction at the three temperatures used.

Compute the time required at each temperature for a complete contraction.

Set the drum moving at its slowest speed. Surround the muscle with Ringer's solution, and without stimulating the muscle allow it to record on the drum while the solution is gradually warmed to 65° C. The contraction brought about by warming above 40° is called heat rigor.

THE NERVOUS SYSTEM

Dissections of PERIPHERAL NERVES may be made according to the description in Reighard and Jennings. By way of suggestion directions for dissecting a typical spinal nerve and a typical cranial nerve are given.

A representative spinal nerve is the great sciatic with its branches. (To be dissected in the cat.)

Cut through the skin on the outer side of the hind leg from the heel to the middle of the back. Remove the biceps femoris muscle. The nerve trunk thus exposed is the *sciatic*. Follow the nerve trunk upward, cutting away overlying tissues where necessary. The nerve can be traced to where it passes through a hole in the pelvic bone. Thrust a seeker through this hole and then cut away the tissues on the front surface of the pelvis until the seeker is exposed. The nerve will thus be brought into view, and can be traced for a short distance to the point where it emerges from the spinal canal.

Returning to the nerve on the outer surface of the thigh follow it downward, noting that it gives off occasional branches to contiguous muscles. A short distance behind the knee the nerve divides into two branches. One of these, the *peroneus*, passes across the gastrocnemius muscle on its outer surface, then plunges beneath it and passes down the shank close to the fibula. It can be followed by cutting away the overlying tissue. The second branch of the sciatic, the *tibialis*, passes directly into the muscular mass of the calf, then turns downward toward the foot. Follow it as far as possible, cutting away overlying tissues carefully.

A Typical Cranial Nerve: The Vagus. Make an incision along the mid-line of the under surface of the body its entire length. Separate the muscles of the neck until the trachea (windpipe) is exposed in the mid-line. Follow around the left side of the trachea, separating the muscles, but not cutting them, until a sheath of connective tissue inclosing blood vessels and nerves is found. This sheath is usually in close contact with the side of the trachea. With a blunt instrument open the sheath and separate the nerves from the adjacent artery for the space of an inch or more. Careful observation discloses two nerves in close contact with each other. The larger is the *vagus*. Follow it toward the head. At the level of the larynx (vocal apparatus) it gives off a branch, the *superior laryngeal*. Continue the dissection forward to the point where the nerve enters the skull. An enlargement, the *ganglion nodosum*, is seen just here.

Return to the point where the vagus was first separated, and carry the dissection backward. Separate overlying tissues, but do not cut through them except when absolutely necessary for progress. At the junction of neck with thorax there are some large

veins which may bleed. If any such are cut accidentally the blood should be carefully wiped away with cotton to keep the field of dissection clear. Follow the nerve into the thorax to the level of the root of the lung. A short distance above this point a branch of the vagus, the *inferior laryngeal*, passes behind a large artery, the aorta, and turns back toward the head.

Branches of the vagus can be traced into the root of the lung. At about the level of the root of the lung the nerve divides into two branches, each of which can be traced to the surface of the esophagus, where each unites with a corresponding branch from the right vagus. The nerve trunks thus formed continue backward along the esophagus to the stomach where they break up into fine branches which supply the stomach and upper portion of the small intestine.

For the CENTRAL NERVOUS SYSTEM the sheep's brain is a satisfactory object of dissection. The brain should be carefully removed from the skull and hardened in formalin (2½–3 per cent) before use (soak in fresh water for at least twenty-four hours before beginning work).

Sheep's Brain. With the aid of the figures on pp. 153, 154, 155, and 159 make out the grand divisions of the brain: *cerebrum*, or fore brain, *midbrain*, overlain in front by the *pons*, and behind by the *cerebellum; medulla oblongata*, forming the connecting link between brain and spinal cord.

Observe on the surface of the cerebrum the irregular *convolutions* which serve to increase its surface relative to its bulk.

On the base of the brain make out with the aid of the figure on p. 159 the *optic tracts* and *optic chiasma;* also as many other roots of cranial nerves as possible. Note that all cranial nerves behind the optic nerve spring from the *brain stem* (midbrain and medulla). In front of the optic tracts and springing from the *cerebrum*, the *olfactory lobes* may be seen.

Cut the brain through the vertical median plane. Note the *corpus callosum*.

Conduction in the Nerve Trunk. The sciatic nerve in the frog can be exposed by removing the skin from the leg and separating carefully the two large muscles on the dorsal surface of the thigh. Dissect the nerve out carefully from the upper end of the leg toward the knee. Use great care to avoid injuring the nerve by

stretching or squeezing. Cut the nerve away at its upper end. Leave it in connection below with the muscles of the shank. The ability of the nerve to conduct impulses may be demonstrated by stimulating it as far as possible from the muscles and observing their response. The susceptibility of the nerve to different forms of energy may be shown by stimulating it with forceps (mechanical), a hot rod (thermal), or shocks from a pair of electrodes leading from the terminals of the induction coil (electrical).

The impairment of conductivity by cold may be shown by bringing against the nerve, between the point of stimulation and the muscle, a small test tube filled with cold brine.

Motor Points on the Body. To one terminal of the secondary coil of an inductorium attach a flat electrode which has been wrapped with gauze well moistened with saline solution. Bare the forearm and lay it, palm up, in contact with the electrode. To the other terminal of the inductorium attach a rod electrode. With the use of tetanizing stimuli of moderate strength explore the surface of the forearm by means of the rod electrode. At certain points individual muscles will be thrown into contraction. These points are "motor points."

Spinal Reflexes

Suspend a frog, whose brain has been recently destroyed, by means of a hook through the jaw. Pinch the toes of the right foot. The foot is retracted. Repeat the experiment on the other toes. In each case note the relation of the muscles that respond to the region stimulated.

Tie two fine copper wires ¼ inch (6 mm.) apart, about the right hind toes. Carry these to the terminals of the secondary coil. Send in tetanizing shocks of increasing strength. As more and more widespread movements are elicited note the order in which various parts of the body become involved.

Moisten a bit of porous paper with acid. Place the acid on the frog's back near the legs. Note the adaptive response.

Wash the skin thoroughly with water. Repeat the experiment, this time placing the acid paper on the belly.

Destroying the frog's brain has destroyed his intelligence. These responses, though adaptive, are purely automatic.

By means of a fine-pointed pipette introduce a few drops of

strychnine solution under the skin of the frog's back. After allowing a few minutes for the drug to take effect pinch one of the toes.

The widespread convulsive responses signify the equalizing of synaptic resistances (p. 172).

Summation and Inhibition of Reflexes

Summation. Suspend a frog, whose brain has recently been destroyed, by a hook through the lower jaw. Tie fine copper wires ¼ inch (6 mm.) apart, about the right toes. Connect the wires with the secondary coil of an inductorium, taking care to avoid short-circuits. The primary circuit should be arranged to give single shocks.

Set the secondary coil so that a small twitch follows each stimulus. Make and break the primary circuit repeatedly and rapidly.

Note that a series of stimuli produce an effect that a single stimulus could not. This is *summation.*

Inhibition. Bring dilute acid in a beaker in contact with the left toes of the frog used in the preceding experiment.

Determine in seconds the time required for the foot to be withdrawn.

Immediately wash thoroughly with water the acidified foot.

Now bring the beaker of acid again in contact with the left toes, *at the same time* stimulating the right toes with an interrupted current of moderate strength.

Determine the time for withdrawal of the foot from the acid. A delay is due to *inhibition.* To prove that the acid has not injured the foot repeat the immersion without simultaneous stimulation. Prompt withdrawal should occur.

Neuro-Muscular Fatigue

Dissect out a gastrocnemius-sciatic preparation (p. 632). Arrange to secure a record of the contraction of the muscle. Moisten the nerve frequently with salt solution to prevent drying and consequent loss of irritability. With the drum moving at a slow speed stimulate the *nerve* of the preparation with fairly strong stimuli until the muscle no longer responds. Now quickly bring the electrodes in contact with the muscle itself. A contraction shows that the muscle is not fatigued.

Since nerve trunks are indefatigable the fatigue must have occurred in the neuro-muscular junctions (p. 211).

Time Relations in Nervous Processes

Determine accurately by repeated trials the time in seconds required for a single revolution of the kymograph drum at its highest speed. Be careful to use this determined speed in the observations below. Each experiment requires a subject and an operator.

Simple Reaction Time. Arrange the inductorium for single shocks, and select a strength of stimulus distinctly felt on the tongue at the break of the primary circuit. The apparatus is so arranged that the operator can make and break the circuit at one place and the subject at another (see diagram, Fig. 162).

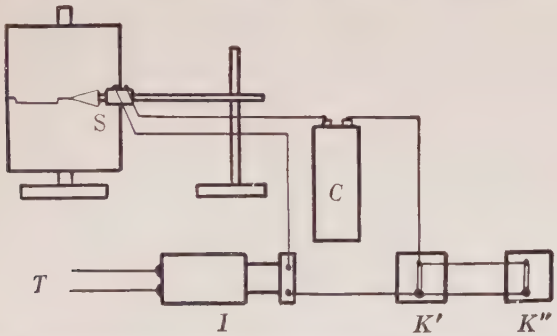


Fig. 162.—Diagram of reaction time apparatus. *K'* and *K''*, keys for making or breaking primary circuit; *C*, dry cell; *I*, inductorium; *T*, wires to tongue electrodes; *S*, signal magnet, writing on drum.

A signal records on the drum the instant of making and breaking the circuit. Let the subject press the electrodes on his tongue, place his hand on his key, and close his eyes. The operator should now start the drum at known speed and close the circuit at his contact. While the drum is in motion the operator should break the circuit at his contact. This break shock stimulates the subject. The instant the stimulus is felt the subject should close his key. The points of stimulus and of response are shown in the record traced by the signal on the drum. Repeat the experiment several times with each member of the pair acting as subject. After the tracing has been varnished measure with care the length of each

reaction record. By comparing these lengths with the drum circumference compute the reaction times in hundredths of a second. Average the results from each individual.

Thought Time Compared with Speech Time. With the apparatus arranged as before let the subject, when stimulated, think the first ten letters of the alphabet before pressing his key. Repeat the experiment; this time having the subject say the ten letters aloud. Make a number of trials and determine the average results.

THE SPECIAL SENSES

In the following experiments one member of a pair is to act as subject, the other as experimenter. Members of the pair should alternate in these functions.

Touch

Localizing Delicacy. Let the subject sit with his hand on the table, and with eyes closed. Apply carefully to the back of the hand the points of small dividers separated about ½ mm. The subject reports whether he feels one point or two points, or is in doubt. Record the result. Change the distance between the points gradually, in successive tests applied to the same region, until the subject reports a change in sensation. The minimal distance at which the two points can be felt as two points is the threshold.

Record the results of testing for the threshold on the finger-tips, palm, flexor and extensor surfaces of the forearm, cheek, and lips.

Temperature

Cold and Warmth Spots. Outline an area on the back of the wrist about 2 cm. square. Let a blunt pointed metal rod stand in cold water until it has become cooled. Dry it and examine point by point the selected area. Mark the spots at which the cool rod causes sensations of cold.

Let the rod stand in hot water until it can be felt as hot when dried and touched to the skin lightly, but not so hot as to cause burning or pain. Explore point by point with very light contact an equal area contiguous to that examined for cold spots. Mark with ink the spots at which the rod causes sensations of warmth.

Equilibrium Sense

Compensating Movements. Let the subject with head erect rotate his body for 15 seconds about the vertical axis. When rotation is stopped, note the movements of the eyeballs and the arms and legs. Describe the after-sensation.

Influence of Vision on the Maintenance of Equilibrium. Try to stand on one foot for a minute with the eyes closed. Repeat the trial with the eyes open. Record the experiences.

Hearing

Threshold. In a quiet room determine the greatest distance at which the subject, who sits with eyes closed and a hand pressed tightly over the right ear can hear the ticking of a watch held opposite the left ear. Repeat the experiment with the right ear, holding the left ear tightly closed.

Bone Transmission. Hold a ticking watch between the teeth. Close both ears with finger-tips. Note the effect on loudness of closing both ears.

Unstop one ear. Compare the loudness in the two ears.

Space Perception. Let a student click together two coins in various positions with reference to the ears of another student, who acts as subject and keeps his eyes closed. The subject should point in the direction to which he refers the sound. Compare the accuracy of judgment at the sides with that in the median plane.

With a finger-tip stop the ear on one side, and observe whether the power of localizing sound is diminished.

Taste

Localization. Apply to different parts of the tongue samples of the following solutions: a solution of quinine sulphate (bitter), a 5 per cent solution of cane sugar (sweet), a 10 per cent solution of NaCl (saline), and a 1 per cent solution of acetic acid (sour). Note the region on the tongue on which each substance is tasted most acutely.

Let the student wipe the surface of his tongue as dry as possible, and then let another student apply crystals of salt and of sugar to the dry surface.

Undissolved substances are not tasted.

Smell

Fatigue. With one nostril stopped, smell tincture of iodine through the other. Hold the bottle near the nose, inhale evenly and somewhat rapidly, and exhale through the mouth.

Note the time required to produce exhaustion.

Allow a minute for recuperation and repeat the above test. Repeat until a minute does not suffice for recuperation.

Note the successive exhaustion times.

This experiment explains failure to perceive closeness in a room through fatigue of the sense of smell.

Vision

A good introduction to the study of vision is the dissection of the eye.

Sheep's eyes hardened in formalin are satisfactory. Directions for dissection are given below.

Conjunctiva. This is the smooth membrane which is loosely attached to the eye in front. It lines the lids, and is reflected from the lid upon the surface of the ball.

Muscles. Remove the fat which is adherent to the ball, so that the external smooth coat will be exposed. The cut ends of several muscles will be seen.

The Cornea and Sclera. On the free surface of the ball the elliptical area includes the cornea, transparent during life but rendered opaque during preservation; the rest of the surface of the ball is constituted by the naturally white and opaque *sclera*, commonly called the *sclerotic coat.*

Optic Nerve. With the finger and forceps tear apart the muscular masses surrounding the optic nerve, and remove with the scissors. Notice the fibrous constitution of the nerve and the firmness of the sheath; also, that the nerve does not enter the center of the eye.

Aqueous Humor. Press the eye so as to make the cornea tense. Cut through the cornea with the point of the scalpel; a clear fluid will ooze out.

Iris and Pupil. Raise the cut edge of the cornea with the forceps and remove it with the scissors; a dark lamina, the *iris*, with a central orifice, the *pupil*, will be seen.

Anterior Chamber. This is the space between the iris and cornea and is filled with the aqueous humor. Through the pupil will be seen the *crystalline lens.* The space between the iris and the lens is called the *posterior chamber* and also contains aqueous humor.

The Crystalline Lens and the Coats of the Eye. Make a median section through the remaining part of the eye. The lens in cross section, the cut edges of three coats, and a transparent jelly-like mass, the *vitreous humor*, will be seen.

The coats from within outward are:

1. The *retina*, a very thin, white membrane, covering the inside of the eye, except the anterior part. The retina is a continuation of the optic nerve. At its posterior part where the nerve enters may be seen a small area, the *blind spot*, from which several minute blood vessels radiate.

2. The *choroid coat*, which is the middle tunic of the eye, is pigmented, and firmer than the retina. This coat appears black or blue in the specimen, and is continued into the *ciliary body* and the iris, the former supporting and controlling the shape of the lens in accommodation.

3. The outer coat is the *sclera*, the anterior part of which is transparent and called the *cornea.* It is thick and fibrous, giving strength and form to the eye. It is white in appearance, is pierced by the optic nerve at the back, and gives attachment to the muscles on its outer surface.

Lens. Separate the halves of the lens from the vitreous humor in which they are imbedded. Note that the lens is composed of concentric layers, like an onion. It is surrounded by a capsule. Note that the anterior surface is flatter than the posterior.

Refraction in the Eye

The eye is an instrument for producing upon a sensitive surface, the retina, images of objects in space. The production of an image requires a device for *focusing.* In the eye the cornea and lens together make up the focusing apparatus. The eye is so constructed that rays of light coming from points more than 18 feet away are focused naturally upon the retina.

The fundamental fact of vision, the formation of images by lenses, can be demonstrated with the aid of a double convex lens, a candle flame, and a screen in a darkened room. The visual de-

fects of *myopia* and *hyperopia* (p. 277) may be illustrated by shifting the screen in such a manner as to throw the image on it out of focus. When the screen is too far away from the lens for the image to be clear the situation is as in myopia. A double concave lens placed in the path of the rays illustrates the correction for this defect. Throwing the image out of focus by bringing the screen too near the lens gives the situation seen in hyperopia. This may be corrected with a double convex lens.

Some Phenomena of Vision

Visual Reference. The eye learns by experience to refer visual stimuli outward through a point called the "*nodal point*" (p. 283). This point is within the crystalline lens, three-quarters of the distance from retina to cornea.

Scheiner's Experiment. The fact that images on the right side of the retina are interpreted as coming from objects to the left of the visual axis, and vice versa, was demonstrated by Scheiner in 1619.

Pierce a card with two pinholes about one-tenth inch apart. Look through the pinholes at a distant object. Place in the line of vision about a foot from the eye a pin mounted in a block. Do not accommodate for the pin. Two images of the pin are seen. Slide a card over the right hand pinhole. The *left hand* image disappears.

Place the pin four feet from the eye. Look through the pinholes at a second pin in line with the first one, but only four to six inches distant from the eye. Two images of the far pin are seen. Slide a card over the right hand pinhole. Now the *right hand* image disappears. For the explanation see diagram, Fig. 163.

The Blind Spot. Make a small black spot near the left margin of a sheet of note paper. Place the paper on the desk. Let one student of a pair look fixedly at the spot with the right eye, holding the head stationary, about twelve inches over the spot. The other member of the pair should move a black-headed pin from a point in the right margin of the paper directly opposite the black spot toward the spot itself. The subject should report the instant the head of the pin disappears, and the place should be marked with a pencil. Continue moving the pinhead toward the black spot and fix in the same manner the place of reappearance of the

head of the pin. These two spots indicate the lateral extremities of the *blind spot*. Its outline is to be determined by moving the pinhead toward it from various directions and fixing the point of disappearance in each of them.

The Field of Color Vision. Let one student of a pair look fixedly with the right eye at a spot in an upright screen, supporting the chin firmly. The other student moves a small square of colored

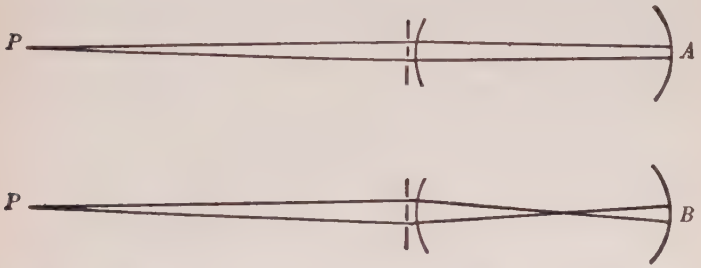


FIG. 163.—Diagrams illustrating Scheiner's experiment. In *A* the eye is accommodated for distant vision and rays from the pin *P* strike the retina before they meet. The image through the *right hand* pinhole falls upon the *right hand* side of the retina, just opposite to the usual manner. In *B* the rays cross before striking the retina. The relation of images to pinholes is therefore the same as in ordinary vision.

paper toward the "spot" from the margin of the screen. The squares of paper should be fixed to straws or stiff wires so they can be handled readily. Red, green, blue, yellow, and white should be the colors provided. The subject should not know which color is being used. As soon as he recognizes the color he should report it, and the color should be marked on the screen. If the color is incorrectly named, continue moving the square inward until it is correctly perceived. Repeat the test along different meridians and with different colors until the field of each color has been roughly outlined.

BLOOD

Histological Structure. Blood is composed of a liquid, the plasma, in which are several kinds of minute structures, the *corpuscles, red* and *colorless,* and the *platelets.*

A sample of blood for observation is prepared as follows: Provide two clean microscopic slides. Congest the blood in the middle finger of the left hand by wrapping a handkerchief tightly about

it, beginning at the base. Prick the congested region sharply with a clean needle and squeeze out a drop of blood. Bring the surface of one of the slides near one end in contact with the drop of blood. The blood will adhere to the slide. Quickly place an edge of the second slide against the surface of the first one and move it along till it comes in contact with the blood-drop. The latter should spread out along the edge of the second slide. Now draw this slide along the first one. The blood will follow, and thus be spread out in a thin layer. Let the slide dry for a few minutes before beginning observations. No cover glass is needed, but the slide should be kept free from dust.

Place the prepared slide on the stage of the microscope and focus on it with the low power. Numerous pale yellow specks will be seen. These are *red corpuscles*. Some idea of their great numbers in the blood can be gained by comparing the area of the field of the microscope with that over which the original blood-drop was spread, and that drop, in turn, with the whole volume of blood in the body.

Change from the low-power objective to the high power. Note that by this change the field is much reduced. After obtaining a sharp image, study individual red corpuscles carefully. Compare the margin of a corpuscle with its center. The different appearance of the two regions signifies that the corpuscle is a disk thicker at the edges than in the center.

Look for groups of corpuscles arranged in rows, edge to edge. These are *rouleaux*. Corpuscles in shed blood tend to cling together thus.

By exploring the slide carefully, *colorless corpuscles* can be found and studied. They are transparent, colorless bodies about twice the diameter of red corpuscles. They are much less numerous than red corpuscles. The ratio is about 1 to 800.

The various kinds of colorless corpuscles can be distinguished by their appearance after treatment with suitable stains. On prepared slides different types of colorless corpuscles can be studied.

Chemical Structure. Blood-plasma * is an exceedingly complex liquid. It carries in solution all substances absorbed from the diges-

* The liquid part of clotted blood is called serum. That of unclotted blood is called plasma.

tive tract; all waste products of cell activity; all hormones; and all of the great group of unidentified materials concerned with the control of infection. The most prominent constituents of blood belong in the chemical group of proteins.

Tests for Blood Proteins. The Xanthoproteic Reaction. Pour in a test tube concentrated blood serum to the depth of $\frac{1}{4}$ inch. Add 3 or 4 drops of concentrated nitric acid (HNO_3). (Handle with care.) Boil and cool. A yellow precipitate is formed and the solution becomes yellow. Add strong sodium hydrate (NaOH). (Handle with care.) When sufficient has been added the color becomes much deeper.

The Biuret Reaction. Pour a little blood serum into a test tube. Add a few drops of very dilute copper sulphate ($CuSO_4$). Make alkaline with sodium hydrate (NaOH). A rose color is produced. These two tests are characteristic for proteins.

Iron in Hemoglobin. The essential substance of red corpuscles is an iron-containing pigment compound, hemoglobin. The property of hemoglobin as an oxygen-carrier depends on its iron content.

A Chemical Test for Iron. Place a few iron filings in a test tube. Pour into the test tube, under a hood, a few drops of aqua regia (nitric and hydrochloric acids). The fumes of aqua regia are very irritating and the fluid is very corrosive. Handle with great care, always under a hood, and avoid inhaling the fumes. After allowing a few minutes for some iron to be dissolved, dilute with an inch of water and add a few drops of potassium ferrocyanide solution. A characteristic *deep blue* precipitate of iron ferrocyanide (prussian blue) is the test for iron.

To demonstrate the presence of iron in blood, place a few lumps of dried blood in a porcelain crucible over a bunsen flame under a hood. Continue heating the mass, stirring occasionally with a glass rod, until only a reddish ash is left. Allow the crucible to cool. Add a few drops of aqua regia. Warm gently. After the solution has cooled again dilute with water, pour into a test tube and add potassium ferrocyanide solution. The appearance of abundant prussian blue shows the presence of iron in the ash of blood.

Coagulation of Blood

Draw a drop of blood, as described above, but do not remove it from the finger. Rest the hand in a comfortable position. Test the consistency of the blood-drop by drawing a hair through it. Repeat the test at intervals of one minute till no further change occurs. Observe the changes that take place in the drop of blood during the process of coagulation.

Coagulation Time. When blood clots it sets first into a soft jelly which is firm enough, however, to support a small weight. Advantage is taken of this fact in the *Dale Coagulometer.* A fine glass tube, about $\frac{1}{2}$ inch long, is to be filled, by suction, with freshly drawn blood. A small shot placed in the tube will run along it when the tube is inclined so long as the blood is uncoagulated, but will remain stationary as soon as clotting occurs.

Congest the finger as above, and after two sharp prickings with a needle, near together, squeeze out a good sized drop of blood. Suck the fine tube nearly full. Insert the small shot as quickly as possible. The ends of the tube need not be plugged, since surface tension will retain the shot in the blood. Note the minute and second at which the blood was drawn. Thirty seconds thereafter hold the tube upright with the shot at the top. If the shot runs down repeat at thirty second intervals until it fails to move. The elapsed time is coagulation time. To check the result the experiment may be repeated.

The Importance of Calcium in the Coagulation Process. Prepare to repeat the above described experiment on coagulation time. *After the blood is drawn and before sucking it into the tube* sprinkle into it three or four grains of powdered sodium oxalate. This substance removes the calcium from the blood by precipitation. Continue the experiment for twice the coagulation time previously determined. If the blood has not then clotted discontinue the experiment. Interpret the result.

Coagulation Time in a Lower Animal. The experiment on coagulation time may be varied by using, instead of human blood, blood drawn directly from the vessels of a turtle (with brain destroyed and plastron removed) into the tube of the coagulometer. Determine carefully the coagulation time for the turtle. Compare with the coagulation time of human blood.

THE CIRCULATORY SYSTEM

A good introduction to the study of the circulation is the dissection of the chief arteries and veins of the cat.

Preparation. Inject the arterial system with a starch mass colored red. To do this expose the heart and tie the nozzle of the injecting syringe directly into the tip of the left ventricle. The injection drives the blood into the veins so that they retain their natural blue color. Trace the vessels by tearing cautiously with the handle of a scalpel or some blunt instrument. Do not cut unless directions are given. Lay the thorax and abdomen wide open by a median incision.

Heart. The process of injection mutilates the heart. A separate exercise on the sheep's heart is described below.

Arteries of the Thorax

The Aorta. This is a single great artery arising from the left ventricle of the heart. It curves sharply to the left, thus making the *arch* of the *aorta.*

Coronary Artery. Two in number arising within the heart; they are small and the first branches seen. They supply the heart.

Innominate. This arises from the convexity of the arch very near its origin; it gives rise to the *right* and *left* carotid arteries.

Subclavians. The *right subclavian* is a continuation of the *innominate*; the *left subclavian,* the next large branch of the aorta, is given off close to the innominate.

Intercostal Arteries. These are seen, one below each pair of ribs.

Arteries of the Abdomen

Abdominal Aorta. This is a continuation of the thoracic aorta. Turn the stomach and intestines to the right, press upon the median line against the spinal column, and the injected aorta will be felt. Tear away the peritoneum and follow the vessel from the diaphragm and note branches.

Celiac Axis. As the aorta enters the abdomen there is given off a large branch, the celiac axis. This divides into three branches, the first being the *gastric,* which goes to the stomach. The second goes to the liver and is called the *hepatic artery.* Turn the liver

upward, and near the lesser curvature of the stomach this vessel will be seen. The third and largest is the *splenic*.

Superior Mesenteric. Turn the stomach and intestines to the right. The artery rises from the aorta just below the celiac axis. It has an extensive distribution to the coils of the small intestine.

Renal Arteries. Rise from the sides of the aorta and enter the hilum of the kidneys.

Inferior Mesenteric. It arises from the abdominal aorta about opposite the iliac crest, and has two large branches which supply the large intestine.

Arteries of the Lower Extremity

Just before leaving the abdomen the aorta sends off four branches, two *external iliacs* and two *internal iliacs*, and then it becomes the caudal.

External Iliac. This passes downward a short distance and becomes the *femoral artery*, it runs down the leg as the *femoral*, and behind the knee it becomes the popliteal, which divides into the *anterior* and *posterior tibial*. The *anterior tibial* becomes the *dorsalis pedis* on the upper surface of the foot.

Internal Iliac. This arises from the aorta just below the origin of the preceding and passes obliquely downward into the pelvis, and supplies the organs of the pelvis with the following branches: *vesical* to bladder, *internal pubic* to internal genital organs, *external pubic* to external genital organs, *sciatic*, with gluteal branch, to muscles of back of pelvis, hip, and thigh.

Caudal Artery. A continuation of the aorta to the tail.

Arteries of the Head and Upper Extremities

Carotid Arteries. These arise from the innominate artery, a short distance above the arch of the aorta, and pass upward on either side of the trachea, supplying the neck and head. Follow one of these arteries forward, noting its branches.

Subclavian Arteries. The right subclavian is a continuation of the innominate. The left arises from the arch of the aorta. They supply the upper extremities. Follow the artery down one arm, note the *vertebral*, a branch running up the foramina in the transverse processes of the cervical vertebræ to the brain. The sub-

clavian changes its name to *axillary* in axilla, *brachial* in upper arm, and divides at elbow into *radial* and *ulnar*.

These arteries give off branches to muscles and surrounding tissues in their course.

Veins of the Extremities

These veins follow the general course of the arteries and usually have similar names in their corresponding positions.

Common Iliac Veins. These form the inferior vena cava at a point opposite the junction of the sixth and seventh lumbar vertebræ, where the internal and external iliac veins which bring the blood from the leg and pelvis unite to form the common *iliac vein.*

Inferior Vena Cava. This is formed by the union of the common iliacs. Turn stomach and intestines to the left. It will be seen accompanying the aorta, and running to the right auricle of the heart.

Renal Veins. These extend laterally from the kidneys and empty into the inferior vena cava.

Portal Vein. Formed near the outlet from the stomach by union of veins from the stomach and intestines, and goes to the liver.

Veins of the Thorax. The *superior vena cava* is a prominent vessel extending from a point opposite the first rib to the upper part of the *right auricle.* It conducts the blood from the head and upper extremities back to the heart. It is formed by the union of the two *innominate veins.*

Innominate. Formed by union of the *subclavian* and *jugular* veins.

Subclavian. This returns the blood from the arm.

External Jugular. Returns the blood from head and brain.

ANATOMY OF THE SHEEP'S HEART

Removal of the Pericardium. At about the middle of the length of the heart, slit the pericardium and with the scissors girdle it completely. Remove the lower portion and note the smoothness of its internal surface. It and the apposed external surface of the heart are covered by a serous membrane which secretes a fluid during life. Turn the upper portion of the pericardium inside out, like the finger of a glove. At varying distances from the base it is attached to the heart and vessels. Trim the pericardium along or near the line of attachment.

General Topography of the Heart. The apex is conical, smooth, firm, and fleshy, and is formed by the muscular *ventricles.* Notice that the left ventricle is larger and has thicker walls than the right ventricle. The base is irregular and wider. It presents not only the thin-walled auricles but also vessels and fat.

The Vessels. The *aorta* and *pulmonary artery* maintain a cylindrical form and their cut ends are naturally circular. The great veins have thinner walls in proportion to their size and collapse more or less completely. The *inferior vena cava* forms nearly a right angle with the long axis of the heart. The *superior vena cava* is at the base on the ventral surface. The *pulmonary artery* is the prominent vessel on the ventral aspect between the two auricles, extending from the base of the right ventricle. The *aorta,* with its principal branch, will be seen more distinctly at a later stage.

Dissection of the Heart. The order of dissection follows the course of the blood through the organ. Bear in mind that, although anatomically united and acting together as muscles, as to their cavities, the right and left sides of the heart are entirely separated by complete partitions between the two auricles and between the two ventricles. When the cavities are open wash their interiors with running water. The flowing water will show how the valves close the openings between the cavities and also the action of both sets of semilunar valves.

Opening the Right Auricle. Hold the heart with its ventral side toward you. Push the point of the scissors into the upper and outer angle of the appendix and cut toward the median line of the heart. Lift the edge of the flap and note the wide mouths of the great veins. The right, the *superior;* the left, the *inferior vena cava.* In the back wall of the auricle at the base of the inferior vena cava will be found an oval scar, the *fossa ovalis.* Near the orifice of the inferior vena cava is a ridge, the *eustachian valve.*

Opening the Right Ventricle. This must be done very carefully. At a point on the ventricle at a short distance from the pulmonary artery, insert the point of a scalpel and cut parallel with the furrow extending to the apex of the right ventricle. Keep the cut edges of ventricular walls apart while studying the cavity.

Musculi Papillares. These are muscular columns attached at one end to the walls of the ventricle, and at the other to the *cordæ tendineæ.* These are delicate tendinous cords which pass from

the musculi papillares to the edge of the valve segments. The muscles and cords prevent the segments of the valve being forced into the auricle by the pressure of the blood behind them.

The Tricuspid Valve. Pass the finger from the auricle into the ventricle and distend the *auriculo-ventricular orifice.* Note that it is surrounded by three fibrous sheets which hang down into the ventricle and are connected at the sides to the *musculi papillares* by the *cordæ tendineæ.* This is the *tricuspid valve.*

The Pulmonary Artery. With the scissors, extend the incision upward through the pulmonary artery and note that the mouth of the artery is surrounded by three membranous cups, the *semilunar valve.* Each constitutes a sort of pocket, and all three together when distended close the opening of the artery completely.

Opening the Left Auricle. Make an incision in the appendix so as to see the interior of the auricle. Note the two portions, the *appendix* and the *atrium.* It resembles the right auricle.

The Pulmonary Veins. Hold the heart so as to see the depth of the atrium and note that it presents a ridge at right angles to it. Hold the organ to the light and note the openings of the pulmonary veins near the ridge.

Opening the Left Ventricle. With the scalpel transect the left ventricle, carrying the incision to the apex. The left ventricle forms the apex of the heart. The *auriculo-ventricular opening* of this side is surrounded by the *mitral* or *bicuspid* valves. Note the *cordæ tendineæ* and *musculi papillares.*

The Aorta. Pass a probe into the aorta and follow the course of the probe with the scissors, thus opening the aorta. Note the *semilunar* valves guarding its orifice. Note the openings of other blood vessels from the aorta, the *coronary arteries,* just above the valve. Observe the smooth lining of the aorta, as well as of the auricles and ventricles.

THE CIRCULATION OF BLOOD IN THE FROG'S FOOT

A live frog is wrapped carefully in moist cloth except one leg. The projecting foot is secured on the microscope stage in such fashion that a portion of the web is in the field. Study the field with the low power.

Note the rate and character of the blood flow in different vessels. The larger vessels are either *arteries* or *veins*. In arteries the blood flow is intermittent, and the rate of pulsation agrees with that of the heart-beat. In veins the flow is more or less steady. The smallest vessels are capillaries. These communicate, in general, between arteries and veins. In the frog's web, however, the circulation is anastomosing. In such a circulation some capillaries can be seen connecting one vein with another. The direction of flow in anastomosing capillaries is sometimes forward, and sometimes backward.

Study a region showing arteries, veins, and typical, nonanastomosing capillaries.

THE CIRCULATION OF BLOOD IN MAN

Pulse Tracings. To obtain a graphic record of the pulse the pressure changes in the beating artery are transmitted to a delicate recording device known as a tambour. For the transmitter a thistle tube, with sheet rubber tied tightly, without stretching, over the mouth, may be used. Secure a bone or wood button to the center of the rubber. Connect the transmitter with the recorder by a rubber tube. Insert in the course of this tube a glass T with a short rubber tube on the side neck.

Gently press the button on the transmitter on the front surface of the wrist directly over the point where the pulse can be felt in the radial artery. The carotid artery in the neck may be used if preferred. When the system is made air-tight by closing the side tube the tambour lever should pulsate in synchronism with the artery. Obtain a record of these pulsations on a drum moving at moderate speed. The notch in the descending limb of the pulse curve marks the closing of the semilunar valves, and therefore the end of systole.

Determinations of Pulse Rate. In these determinations two students should alternate as subject and observer. Trustworthy readings cannot be made upon oneself. The pulse should be taken by pressing the tips of three fingers against the radial artery at the wrist. Do not use the thumb.

With the subject sitting quietly in a comfortable position count the pulse during the first twenty seconds of three con-

secutive minutes. Compute the rate per minute for each minute. If there is much variation wait three minutes and try again for three minutes. When the pulse is reasonably steady for three consecutive minutes the average rate may be taken as the pulse rate for that subject in that particular condition.

The Effect of Posture. Using the method described above determine the pulse rate with the subject lying down, sitting, and standing.

The Effect of Exercise. Determine the pulse rate with the subject in the sitting position. When the rate is uniform let the subject raise and lower his legs six times without rising from his seat. Count the pulse for twenty seconds as quickly as possible after the movement ceases.

This shows the effect of slight exercise.

After the pulse rate has returned to normal and become steady let the subject run up and down stairs for two or three minutes. Count the pulse for twenty seconds as soon as possible after he returns to his seat and at two-minute intervals for ten minutes thereafter.

This shows the effect on pulse rate of vigorous exercise.

The Direction of Blood Flow in Arteries and Veins. Expose the arm to the shoulder. Find in the upper arm a place where the pulse can be felt. Learn by practice to occlude the artery by pressing it against the arm bone. Now with one hand on the artery in the upper arm and the other on the artery at the wrist determine the direction of arterial flow by showing which pulse disappears when the other artery is occluded.

Occlude a prominent vein on the hand or forearm by pressing upon it with a finger.

Observe on which side of the occluded point the vein becomes congested.

Attempt to empty the vein above and below the occluded point by pressing a finger along it.

Note on which side of the point this can be done.

Thus is determined the direction of venous flow.

The Control of Hemorrhage. Bleeding can be checked by compressing the ruptured blood vessel on the side of the injury from which blood comes.

Arterial bleeding can be distinguished from venous by the

brighter color of the blood and by the fact that the blood escapes in jets. When bleeding is from veins the flow is steady and the blood is dark.

Veins which are likely to be injured are on the surface. A bandage tied tightly around the arm or leg in proper position relative to the injury usually suffices to check venous bleeding. Select a point on the arm as a possible seat of injury. Adjust a bandage in such a position as to cut off venous flow to the chosen point. Show on a diagram the position of injury point and of bandage. Indicate direction of venous flow by arrows.

Arteries are deep seated through most of their course, and blood pressure within them is high. To check arterial bleeding strong pressure on properly selected points is necessary. Expose the entire arm. Find a point near the upper and inner margin of the biceps muscle where the pulse can be felt. Strong pressure on this point if properly applied will check arterial bleeding below. For a more permanent check make a hard knot the size of an egg in the middle of a handkerchief. Tie firmly around the arm just above the elbow with the knot in front. Bend the forearm so that it presses hard against the knot. If the procedure is successful the pulse at the wrist disappears. Another method is to make a hard knot of cloth the size of a fist. A round stone or other hard substance may be used. Push it hard into the armpit. Bring the elbow straight down and hold it firmly against the side. The success of the procedure should be tested by observing whether the pulse at the wrist disappears. (For the control of bleeding in other regions than the arm see Dulles: *Accidents and Emergencies*, Philadelphia, 1899.)

The Effect of Muscular Movement on Venous Flow. Tie a cloth tightly about the arm at the elbow. Note the rate at which the superficial veins become congested. Loosen the cloth until the veins return to normal. Replace the cloth about the arm and close and open the hand several times.

Compare the rate of venous congestion with that seen in the quiet arm.

HEART BEAT AND BLOOD PRESSURE IN THE TURTLE

A turtle whose brain has been destroyed and plastron (lower shell) removed, is fastened to a board back down, and with neck extended. The *heart* can be seen beating through its inclosing membrane, the *pericardium*. With a fine scissors cut away the pericardium, taking care not to injure the heart. The turtle has two *auricles* and a single *ventricle*. Identify these. Determine by careful observation the sequence of beat of the different chambers.

Compare the periods of systole and diastole.

In the turtle the great veins pulsate as well as do auricles and ventricle. To observe these veins the ventricle must be lifted out of the way. Find the connective tissue *frenum* which attaches the tip of the ventricle to the pericardium. Cut this as far from the heart as possible. Seize the frenum with a pair of forceps and by means of it lift the ventricle till the underlying veins can be seen. The beat is seen to originate in these veins whence it sweeps over the heart in the form of a wave.

Vagus Inhibition. Find the carotid artery where it passes up the neck. Associated with it is a nerve, the vagus. Expose carefully a short portion of this nerve and stimulate it with repeated induction shocks. In a normal preparation one or the other vagus nerve contains inhibitory fibers whose stimulation will stop the heart.

Note whether the standstill occurs in systole or in diastole.

Graphic Record. Catch a pin-hook either through the frenum or through the very tip of the ventricle. Connect this hook by thread or fine wire to the short arm of the heart lever, which should be directly above the heart. Obtain on a slowly moving drum a record of the heart beat. While the record is being traced stimulate the vagus nerve. Indicate on the record the period of stimulation.

Determine carefully the interval between the beginning of stimulation and the cessation of beat. Note also how long it takes the heart to recover after cessation of vagus stimulation.

The Effect of Nicotine. By means of a camel's-hair brush apply a few drops of nicotine solution to the surface of the heart. In

two minutes repeat the vagus stimulation. The inhibition is no longer effective. The junctions of preganglionic and postganglionic neurons of the vagus path are in the heart tissue itself (p. 370).

Arterial Pressure. Disconnect the heart from the recording lever. If the heart is beating feebly or very slowly bathe with warm water. If no response take a freshly prepared turtle. Trace one of the large arteries to a point at least one inch from the heart. At this point separate the artery carefully from surrounding tissues for another inch. Squeeze the artery shut at the cardiac end of the prepared portion by means of a spring clip. Pass a stout thread around the prepared artery. Fill with salt solution a small L-shaped glass tube, 15 inches high. Hold the solution in the tube by closing the long end. Make a transverse cut halfway through the prepared artery, slip the short end of the glass tube through this out into the artery and tie it in place by means of the thread previously prepared. The tube may now be opened and the clip removed from the artery. The height at which the column of salt solution is maintained measures arterial pressure.

THE RESPIRATORY SYSTEM

Dissection of Air Passages and Lungs of Sheep. Note the large trachea (windpipe) with open rings of cartilage in its wall. Observe carefully the surface of the lung. Note the cellular appearance and the delicate texture. Note the subdivision of each lung into *lobes*.

Inflate the specimen.

Dissection. In one lung, follow the *trachea* down the *bronchus* to its smallest branches.

Starting at the heart follow the pulmonary artery and vein to their finest branches. Use a probe and scissors.

On the other lung tear away the tissues so as to show the interlacing of these vessels. Use the forceps to pick with.

Miscroscopic Study. The final subdivisions of the bronchi, and their terminations in *infundibula* and *alveoli*, are microscopic. Observe in prepared and stained sections the relatively thick walled *bronchioles*, and the extremely delicate walls of the air cells (infundibula and alveoli). The capillaries which run in the alveolar walls cannot be seen in ordinary microscopic sections.

Breathing Movements in Man. The following observations may be made by a group of students on a single subject. Let the latter strip the upper part of the Body to the undershirt. With tne subject sitting erect on a stool observe the chest and abdomen closely during quiet breathing.

Note the general direction of movement of the Body walls during inspiration, and during expiration.

Observe the movements of chest and abdomen during *forced* inspiration and expiration.

Abdominal movements are caused by contraction and relaxation of the *diaphragm.* Explain the relationship.

Costal and Diaphragmatic Breathing. Whereas in normal involuntary breathing the diaphragm and the chest muscles are in action simultaneously, it is possible in voluntary breathing movements to use one or the other at will. Compare abdominal movements in normal breathing and in breathing with the chest held stationary (diaphragmatic breathing). Compare chest movements in normal breathing and in breathing with abdomen held stationary (costal breathing).

Volumes of Respired Air. These are:

1. Volume passing in and out in quiet breathing—tidal air.
2. Volume that can be breathed in after a normal inspiration—complemental air.
3. Volume that can be breathed out after a normal expiration —supplemental air.
4. Sum of above: volume that can be breathed out after forced inspiration—vital capacity.

Determine the supplemental air by blowing into a spirometer after normal expiration. Determine tidal air by blowing into the spirometer after normal inspiration and subtracting previously determined supplemental air. Make several trials. Determine vital capacity by blowing into spirometer after forced inspiration.

Determine complemental air by subtracting combined supplemental and tidal air from above.

Graphic Record of Breathing. For recording breathing an apparatus known as a pneumograph is fastened around the chest so that its volume will be changed by breathing movements. It is connected with a recording tambour which indicates on a kymograph the movements of breathing.

With the pneumograph in place and the back to the apparatus get a record of normal breathing.

Note the rate per minute.

Sip the contents of a glass of water. Observe the effect of swallowing on breathing.

Obtain records of reading aloud, of coughing. Compare these with normal, quiet breathing.

The Control of Breathing. The students of a pair should act alternately as subject and observer in the following tests. Obtain, by counting the breathing movements, the normal rate per minute. Let the subject run down and up stairs. Determine the rate per minute every three minutes till the normal rate is restored.

Determine how many seconds the subject can hold his breath. Note the difference according to whether he begins to hold it at the end of inspiration or the end of expiration.

Let the subject breathe rapidly and deeply for two or three minutes and then hold the breath.

Note the time of holding it as compared with the former trials.

Repeat the experiment, this time breathing into and from a paper bag. Compare the time the breath can be held with former trials.

The automatic stimulus for breathing depends on the amount of carbon dioxid in the blood, and indirectly on the amount in the alveoli of the lungs. The experiments on breath-holding can be explained on this basis.

Artificial Respiration. The Schafer Method. In this experiment the subject should cease breathing so far as possible. The treatment may be considered successful when no active breathing movements are necessary.

Lay the subject prone, with a thick roll of clothing under the chest and the epigastrium. Take a position over or beside the subject's legs, and facing his head. Place the hands on either side over his lowest ribs. Slowly throw the weight of the Body onto the hands, and thus compress the subject's thorax and force air from the lungs. Without removing the hands, release the pressure. The chest by its own elasticity will perform the function of inspiration. Repeat this procedure at the normal rate of respiration until the issue is determined. In case of drowning it may be a half hour before respiration is restored. Schafer's

method is specially applicable to cases of drowning because the face is downwards and water in the air passages readily runs out.

Carbon Dioxid (CO_2) *in Expired Air.* Dip a tube below the surface of a bottle containing limewater (CaO_2H_2). Exhale through the tube. The CO_2 in the expired air combines with the limewater in the bottle and forms an insoluble carbonate of lime ($CaCO_3$) which makes the solution cloudy; later this will settle as a precipitate (powdered chalk).

When present in excess the CO_2 makes the solution acid and the $CaCO_3$ redissolves.

THE DIGESTIVE SYSTEM

Dissection of the Digestive System in the Cat

Exposure of the Viscera. Make an incision the length of the abdomen in the mid line. Separate the edges of the opening so as to get a good view of the abdominal contents.

Peritoneum. This is a membrane lining the abdomen. It gives the abdominal wall a smooth glistening appearance and may be easily separated from the muscles forming the wall. The mesenteries and the ligaments of the liver, the bladder and uterus are formed by duplicatures of the peritoneum.

The Great Omentum. This is a double fold of peritoneum forming a sac which is called the *lesser peritoneal cavity.* It is attached to the posterior abdominal wall and the greater curvature of the stomach. Demonstrate the sac-like character of the omentum by tearing it open. Each wall of the sac is also composed of two layers. Notice the distribution of fat through the omentum.

Spleen. This is a deep red, usually single-lobed organ, situated on the left of the stomach in the great omentum.

Drawing. Make a drawing without disturbing anything, showing position of liver, stomach, spleen, and great omentum covering the coils of small intestine.

Stomach. Turn the left lobe of the liver toward the head and the *abdominal esophagus* will be seen emerging from the diaphragm and entering the *cardiac end* of the *stomach.* The stomach, as a whole, is pear-shaped and curved upon itself. The *great curvature* is at the lower border of the stomach, and has the great omentum attached to it, while the *lesser curvature* is the upper border. The

larger or *cardiac* end is next to the diaphragm. The *pyloric* or smaller end is curved sharply upon itself. It is firm to the touch and appears as an annular constriction.

Small Intestine. Very carefully turn the omentum over toward the thorax. The greatly coiled cylindrical small intestine will be exposed. It is divided into three regions, the *duodenum*, the *jejunum*, and the *ileum*.

Duodenum. This is the first portion of the small intestine along which the *pancreas* extends. It is held rather firmly in position. Into the duodenum empty the common bile duct and the pancreatic duct.

Jejunum. This is an ill-defined portion of the small intestine immediately following the duodenum. It is so called because in man it is often found empty after death.

The Ileum. This is the last part of the small intestine. It terminates in the large intestine, entering it obliquely. At its termination is the *ileocolic valve* which allows the alimentary contents to pass from the small to the large intestine, but not easily in the opposite direction.

Large Intestine. Turn the coil of small intestine toward the left leg. The large intestine extends from the cæcum to the anus. It is divided into five parts,—*cæcum*, *ascending*, *transverse* and *descending colon*, and *rectum*.

Cæcum. This is a somewhat conical blind sac at the beginning of the large intestine. It lies on the right side and in about the middle of the abdominal cavity.

Ascending Colon. This is the part of the large intestine which extends upward from the cæcum.

Transverse Colon. This is a continuation of the preceding. It extends transversely across the abdomen in front of the duodenum and below the stomach.

Descending Colon and Rectum. After extending nearly across the abdomen from right to left, the large intestine passes obliquely downward. The last and straighter part is called the *rectum*.

Pancreas. The pancreas will appear as a pinkish, finely lobulated and elongated body after the great omentum has been turned toward the thorax. It extends from the spleen under the stomach to the pylorus, in the great omentum, and then downward for a short distance along the duodenum in the mesentery.

Mesentery. This is a duplicature of peritoneum supporting the different portions of the small intestine. It is a double-walled membrane and carries blood vessels and lymphatics.

Mesenteric Glands. The so-called mesenteric glands belong to the lymphatic system. They are between the layers of the mesentery and are especially large near the cæcum.

Internal Structure of the Stomach. Open the stomach and wash out its contents. It is composed of a *muscular coat* covered by the *peritoneum*, and an *internal, mucous coat,* which is thrown into folds or *rugæ.*

Interior of the Small Intestine. Open and wash in water. It is composed of three coats like the stomach. It has a velvety feel due to *villi,* which are microscopic finger-like processes found only in the small intestine and most abundantly in the upper part.

Interior of the Cæcum. Open the cæcum and observe the ileocolic valve.

Interior of the Large Intestine. Wash the contents out. The structure of the large intestine is like the small, excepting that it has no villi.

The Liver. The liver is a deep red and multi-lobular organ occupying nearly all the upper part of the abdomen but especially the right side. It is supported in various parts by folds of peritoneum. It is composed of right and left lobes, each of which is subdivided into smaller lobes by fissures. The cystic lobe is one of the divisions of the right lobe near the front, and contains the gall-bladder.

If good sections are available the gross study outlined above may be followed by microscopic studies of the structure of the stomach wall, the small intestine, salivary gland, pancreas, and liver.

STUDY OF FOODS

Carbohydrates. The food carbohydrates are *starch, glycogen, dextrin, double sugars, single sugars.*

The following experiments illustrate tests for the different *carbohydrates,* and the application of these tests to different foods to determine which of the carbohydrates is present.

Test for Starch. To a solution of starch add a drop or two of a solution of iodin. A deep blue color shows the presence of starch.

Various foods such as potato, bread, egg white, may be tested for starch by adding hot water to a small amount of each (solids), and then, after cooling, applying the iodin test.

Dextrin. This is an intermediate product in the conversion of starch into sugar, and during the change different forms of dextrin are produced.

Test for Dextrin. To a solution of commercial dextrin add a few drops of a solution of iodin. A reddish color is the dextrin test.

Tests for glycogen, single sugars, and lactose (milk-sugar) are described above (p. 623). Cane-sugar (sucrose) does not give the Fehling test. It can be split into single sugars (dextrose and levulose) by boiling with a mineral acid, and the sugars thus produced will respond to the Fehling test. Tests for proteins and fats are described above (p. 624).

STUDY OF DIGESTION

Salivary Digestion. Add to an inch of dilute starch solution in a test tube a quarter of an inch of saliva. At four-minute intervals test a few drops of this mixture with dilute iodin solution. Note the time it takes for the appearance of dextrin, and then for the disappearance of the dextrin.

The nature of the final product of the salivary digestion of starch may be shown by keeping a test tube of starch solution and saliva, as prepared above, at a temperature of 40° C. for 30 minutes or more. Fehling's test will show the presence of sugar.

Gastric Digestion of Protein. Gastric digestion proceeds slowly. Allow ample time for the following observation; a good plan is to begin the experiment one day and complete it on the next.

Fill each of four test tubes about one-third full of water. Add to the first a few drops of commercial pepsin solution; to the second ten drops of a 0.5% solution of hydrochloric acid; to the third and fourth both pepsin and acid. Place in each tube a cube of boiled egg white. The cubes should be approximately the same size. Mark the tubes and place numbers one, two, and three in a thermostat at Body temperature, number four in a cool place. Shake each tube at intervals. Several hours later examine all the tubes for evidences of digestion. It will be found that acid pepsin is essential, and warmth desirable for gastric digestion.

Movements of the Stomach. Expose the stomach of a recently

killed frog. Tie a ligature about the pyloric end. Make an opening into the stomach at the cardiac end and by means of a pipette fill the stomach with 0.7% salt solution. Tie a second ligature so as to close the opening into the stomach, and cut the stomach from the Body.

By means of a thread attached to the pylorus hang the stomach so that the cardiac end just dips into a solution of 0.7% sodium chloride and 0.1% sodium carbonate. Look for the peristaltic waves passing over the stomach. Note the time required for a single wave to pass, and the number of waves per minute. This observation is more striking in early fall or late spring than in midwinter when the frogs are in the midst of hibernation.

Absorption from Stomach and from Small Intestine. Lay bare the stomach and intestines of a large turtle whose brain has been destroyed and plastron removed without loss of blood.

Using great care to avoid tearing the mesentery (supporting membrane of stomach and intestines) find the points of union of stomach and intestine and of intestine and rectum. Tie stout threads tightly about these points.

Find the junction of esophagus with stomach. Place a thread about the junction ready for tying. Make an opening into the esophagus above the thread. Introduce into the stomach through this opening by means of a graduated pipette, water to moderate distension. Note the exact amount of water introduced. Withdraw the pipette and tie off the junction with care that no water escapes.

Place a thread ready for tying about the intestine one-half inch below the one previously tied about the point of union of stomach with intestine. Introduce a known amount of water into the intestine through a hole made just above the thread last placed. Tie this thread. Allow absorption to proceed for one hour. At the expiration of the period of absorption cut between the threads tied about the upper end of the intestine and dissect out the stomach and intestine. Empty each into a separate vessel. Compare the amount of water introduced with the amount recovered. If the mesentery is intact and the circulation good the intestine will be virtually empty at the end of an hour. The stomach will contain practically the entire amount introduced. Similar tests may be made with solutions of dextrose.

METABOLISM

The Influence of Muscular Exercise on Carbon Dioxid Production. Make the first observation described below after at least one hour of relative inactivity.

Fill a large wide-mouthed bottle with water and invert over a reservoir of water. Insert a good sized rubber or bent glass tube into the neck of the bottle. Place the other end in the mouth. Hold the nose during each expiration and blow all the expired air into the bottle. Note carefully the number of expirations and the time required for filling the bottle with expired air. Cork the bottle tightly and turn right side up.

Fill a narrow test tube with strong sodium hydroxide solution. Cork. Tie a thread about the test tube and by means of this thread lower the tube carefully into the bottle of expired air. Restopper this bottle tightly and then by jarring it break the test tube, liberating the alkali. Shake thoroughly. The alkali takes up the carbon dioxid. Invert the bottle again over the reservoir of water. *With the neck under water* remove the stopper. Water rushes in to replace the absorbed carbon dioxid. Lower the bottle till the water is at the same level inside and outside. With the bottle in this position replace the stopper. The volume of water inclosed equals that of the carbon dioxid in the entire bottle of expired air. Determine this volume with the aid of a graduated vessel. Calculate the volume of carbon dioxid exhaled with each breath and also the volume exhaled per minute.

Rinse the bottle out thoroughly to remove all traces of sodium hydroxide. Take several minutes of very brisk exercise. As quickly as possible after the cessation of the exercise repeat the experiment above. Care must be taken that all the air expired during the period of collection enters the bottle. The augmented breathing makes this a matter of some difficulty. There are numerous sources of error in this experiment, but if carefully performed it demonstrates a marked increase in the carbon dioxid production per minute with exercise, and a suggestion as to the amount produced.

A Study of Urine. Urine is the chief excretion of the body. It contains the greater portion of the end-products of protein metab-

olism and is also the medium in which the *accessories* of the diet are discharged from the Body.

The chief end-products of protein metabolism are *urea, creatinin, uric acid,* and *ammonia.* Among the chief excreted accessories are (a) inorganic: *water,* and sodium, potassium, calcium, and magnesium chlorides, sulphates, and phosphates; (b) organic: non-nutrient constituents of food which serve to give it flavor; drugs. Examples of this class of excreta are the *purin* bodies, which represent the excreted alkaloids of tea, coffee, and cocoa; and the substance which gives urine its peculiar odor after the eating of asparagus.

Test for Urea. To 15 c. c. of urine add $\frac{1}{2}$ its volume of baryta mixture to remove inorganic constituents which would interfere with the test. Filter. To a portion of the filtrate add a solution of mercuric nitrate, a precipitate forms which is a compound of urea and mercury.

Test for Creatinin. To 8 c. c. of urine add 2 c. c. of a solution of sodium nitro-prussiate, then 1 c. c. NaOH; a red color appears. Boil the solution. The color fades; while boiling add about 1 c. c. of acetic acid; the color changes to blue.

Test for Ammonia. To 4 c. c. of fresh urine in a test tube add a little dry sodium carbonate. Heat. Hold in the neck of the test tube, without touching the sides, a strip of moistened, neutral litmus paper. The blue coloration shows the presence of ammonia gas.

Test for Chlorides. To 4 c. c. of urine add an excess of nitric acid (HNO_3), then a drop or two of silver nitrate solution ($AgNO_3$).

Test for Sulphates. Add to 4 c. c. of urine a few drops of barium chloride solution and then an excess of HCl. The latter redissolves the phosphates, leaving the sulphate of barium alone in the precipitate.

Test for Phosphates. Make 10 c. c. of urine alkaline with ammonium hydroxide (NH_4OH). Heat. The precipitate that forms is a mixture of calcium and magnesium phosphates. Filter. To the filtrate add a small amount of magnesia mixture ($MgSO_4$, NH_4Cl, and NH_4OH in water). Heat. The precipitate is due to the presence of sodium, potassium, and ammonium phosphates.

Test for Purin Bodies. Add to 10 c. c. of urine an excess of magnesia mixture. Filter off the precipitate of phosphates. Add

to the filtrate ammoniacal silver nitrate solution. The precipitate consists of the silver salts of the purin bodies, and will be more abundant after tea, coffee, or cocoa have been taken.

A STUDY OF MILK

This is a secretion of the mammary gland and contains Protein, Fat, Carbohydrate (Sugar), and salts in solution.

The opaque white appearance of milk is due to the presence in it of a protein, *casein*. This may be precipitated out with acid or by the enzym *rennin*. In the latter case the casein combines with some of the calcium of the milk forming *paracasein*.

Fill each of two test tubes $\frac{1}{3}$ full of milk and add an equal volume of water.

To one of the tubes add five drops of hydrochloric acid (HCl); to the other ten drops rennin solution. Allow both tubes to stand in a water bath at body temperature.

After twenty minutes filter the contents of both tubes. Make the following tests on each.

Demonstrate the presence of protein in the precipitate (curd) with the xanthoproteic test.

Test for fat with osmic acid.

Apply the biuret test to a few drops of the filtrate (whey).

Test 2 c. c. of filtrate for sugar with Fehling's test.

Add to 5 c. c. of the filtrate three drops ammonia (NH_4OH), and 5 drops sodium oxalate solution. A white precipitate proves the presence of calcium in the filtrate. A careful comparison of acid whey with rennin whey will show that the former contains more calcium.

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